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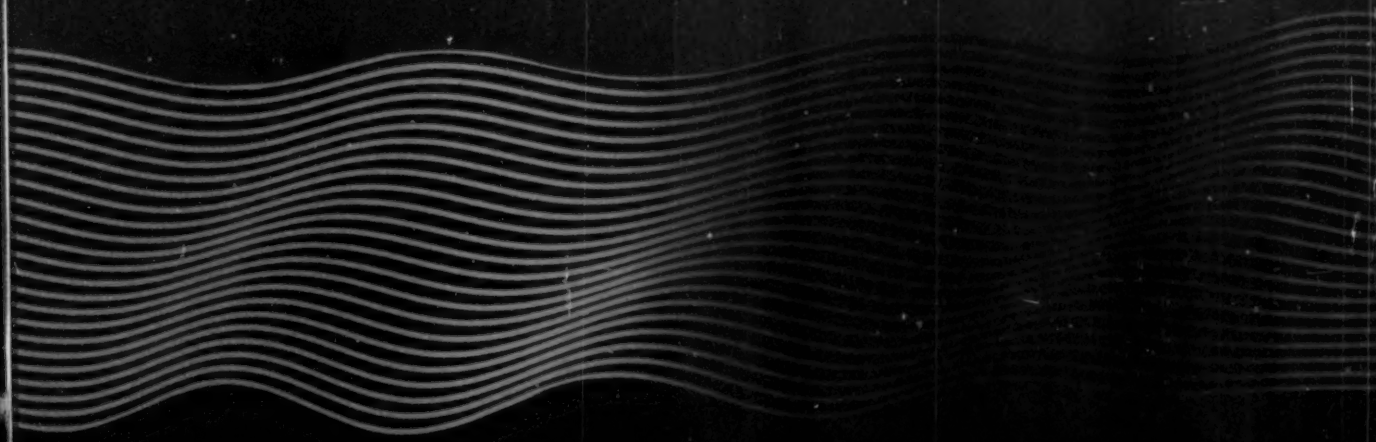

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IN MEMORIAM / NÉCROLOGIE

William Edwin Ricker, OC, FRSC, LLD, DSc

R.J. Beamish, D.J. Noakes, D.L.G. Noakes, and F.W.H. Beamish

In 1973, Bill Ricker retired at the age of 65 from his responsibilities with the Fisheries Research Board of Canada. He had worked 27 years for the "Board", 11 years at Indiana University, and 1 year at the International Pacific Salmon Commission. Over this period and through to his death on 8 September 2001, he produced an amazing array of scientific publications that improved our understanding of nature and helped to found a science needed to manage the developing world fisheries (Fig. 1).

It is difficult to know Bill Ricker. With considerable work, it is possible to identify his many and varied scientific accomplishments. In his personal life, he appeared to be a very private individual. Discussions with his sons and grandchildren produce an understanding of his love for his wife Marion, who predeceased him, and of his devotion to his children and their interests. Bill had a partiality towards young people all his life and this kept him young. He particularly enjoyed being part of the adventures of his sons and their friends, which caused Bill to be very active in the Scouting movement in the 1950s. It seems that this spirit of adventure combined with a love of nature guided a young Bill Ricker into a life of discovery.

Bill Ricker's life is an inspiration to any young biologist contemplating a career in aquatic sciences. Few could hope to make as many contributions, but most could learn from his approach to science. He knew the scientific literature, no matter where it was published. He was clear about his assumptions. He was meticulous and applied good common sense and sound logic. He developed his concepts using simple examples. But most importantly, he communicated the results of his studies to his colleagues. A compilation of his publication includes 296 published papers and books, 238 published translations, and 148 scientific or literary manuscripts (K. Ricker 1998; customercare@accutype.net). Among his publications were 38 papers on stoneflies, which described about 88 new species, including some from outside North America as well as one fossil species. To Bill, every day was a good day to discover something new.

In fisheries, Bill Ricker focused on issues that were vitally important to Canada's commercial fisheries and to the science needed to manage them. However, he also found time to become a world authority in the taxonomy of stoneflies. In fact, it has been noted that some scientists believed that there were two W.E. Rickers as the contribution of the entomologist W.E. Ricker was exceptional for any one person. Bill Ricker described 81 of the total of 617 stoneflies now listed in North America. His interests in stoneflies extended into their zoogeography and evolution. Bill recognised distinctions within accepted genera, which he partitioned into subgenera in his classifications. These subgenera were later considered to be distinct genera. In fact, about one-third of the 101 genera currently recognised in North America were originally identified by Bill Ricker. Fellow entomologists

Fig. 1. William Edwin Ricker, 1908–2001.

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Fig. 2. Bill Ricker on the Canadian research vessel named after him in 1986 with his granddaughter, Andrea, wearing his Order of Canada medal, which he also received in 1986.

Fig. 3. The windswept pine tree atop Mount Benson near Nanaimo, B.C., where the ashes of Bill and Marion Ricker were placed.

wrote that his system of classification was a thing of beauty and simplicity that made evolutionary sense.

In fisheries, he is best known for his 1954 paper on stock and recruitment and his *Handbook of Computation for Biological Statistics of Fish Populations*, first published in 1958. There were 36 of his own papers referenced in the 348-page handbook. His handbook became the standard reference for students and professionals around the world. It is still used in China as the standard text for Fisheries Science. Bill was appointed Editor of the Journal of the Fisheries Research Board in 1950, and during his 12-year tenure, he turned what was a parochial journal into perhaps the world's most influential fisheries science publication. He was a meticulous, but supportive editor. The credibility of the journal was so universal that having a paper accepted was a mark of accomplishment, even before the content was read. It is important to put Bill Ricker's life into perspective. He had one assistant as Editor and did not have other staff to help him collect, store, retrieve, and analyse data. It was during this period as Editor that he wrote some of his most famous papers. One paper that Bill enjoyed writing and believed was important seems to have been forgotten. In his 1969 paper, "Food from the sea", he reasons that the quantity of food available from the sea would be 150–160 million tonnes or

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2.5 times the level in 1968. He shows that other estimates of 100 million tonnes are low and 200 million tonnes too high.

Bill was aware of the accomplishments of the famous Russian fisheries scientist, Feodor Baranov. Bill taught himself Russian while at Indiana University so that he could read Baranov's original papers. He created an awareness of Russian fishery science in the English-speaking community through his published translations and his 428-page Russian–English dictionary on terminology in hydrobiological science for students of fisheries and aquatic biology (Ricker 1973). This dictionary remains the only specialised text on fisheries terminology.

He received about 27 medals and awards including the Flavelle Medal (1970), the Professional Institute of the Public Service of Canada Gold Medal (1966), and the F.E.J. Fry Medal (1983). In 1969, he was honoured by the American Fisheries Society for his superb and original contributions to fisheries science and received their first Award of Excellence. The Society later established the William E. Ricker Resource Conservation Award, which was given to the Pacific Biological Station in 2001. It was a recognition that greatly pleased Bill. Dr. Bill Ricker received honorary doctoral degrees from the University of Manitoba, Dalhousie University, and the University of Guelph. The recognition that he particularly cherished was the naming of the Canadian Fisheries Research Vessel the *W.E. Ricker* in 1986 (Fig. 2), the same year in which he was appointed to the Order of Canada.

On 10 November 2002, family and friends placed the ashes of Bill Ricker under a weathered pine tree on top of Mount Benson just outside of Nanaimo, B.C., the same place where Bill had placed the ashes of his beloved wife Marion (Fig. 3). A small plaque honouring Bill and Marion is mounted on a rock nearby.

Bill Ricker was an unassuming, gentle, humble man. Through his pervasive curiosity and his ability to retain knowledge, he charted a course for fisheries science that opened areas for discovery all around the planet. This was Bill's gift to the young and young at heart. He will be missed but never forgotten.

Acknowledgments

We thank Dr. G.C. Scudder for his summary of Bill Ricker's entomological contributions.

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Genetic control over survival in Pacific salmon (*Oncorhynchus* spp.): experimental evidence between and within populations of New Zealand chinook salmon (*O. tshawytscha*)

Martin J. Unwin, Michael T. Kinnison, Nelson C. Boustead, and Thomas P. Quinn

Abstract: The ability to survive to adulthood and return to natal sites is a fundamental characteristic of anadromous salmonids, and low survival is likely to have prevented establishment of new populations within and outside their native range. We hypothesised that there is family-level genetic variation in traits contributing to survival and that populations evolve to maximise survival in response to prevailing local conditions. To test these predictions, we compared postrelease survival for chinook salmon families from two populations established in New Zealand in the 1900s. Both populations, Glenariffe Stream and Hakataramea River, had similar survival when released after translocation to a drainage familiar to neither population. However, Glenariffe families had higher survival than Hakataramea families when both populations were released from Glenariffe Stream, indicating a survival advantage for the local fish. In addition, there were significant correlations between survival rates for paternal half-sib families of Glenariffe fish and between survival rates for families released from the two locations. Family-specific survival was positively correlated with weight at release, but there were underlying genetic correlations unexplained by size. Taken together, these results suggest considerable genetic influence over survival and return of salmon and that population-specific adaptation can occur within 30 generations of establishment.

Résumé : La capacité de survivre jusqu'à l'âge adulte et de retourner aux sites de naissance est une caractéristique fondamentale des salmonidés anadromes; c'est probablement la faible survie qui empêche l'établissement de nouvelles populations à l'extérieur de leur répartition géographique naturelle. Nous posons en hypothèse qu'il y a une variation génétique au niveau de la famille dans les caractères qui contribuent à la survie et que les populations évoluent de manière à maximiser leur survie en fonction des conditions locales dominantes. Pour éprouver ces prédictions, nous avons comparé la survie après la libération de familles de saumons quinnat de deux populations établies en Nouvelle-Zélande dans les années 1900. Les deux populations, celle du ruisseau Glenariffe et celle de la rivière Hakataramea, avaient des taux semblables de survie lorsqu'elles furent transportées et relâchées dans un bassin hydrographique inconnu des deux populations. Cependant, les familles de Glenariffe avaient une meilleure survie que les familles de Hakataramea lorsque les deux populations ont été relâchées depuis le ruisseau Glenariffe, ce qui indique un avantage de survie pour les poissons locaux. De plus, il y avait des corrélations significatives entre les taux de survie des familles de demi-frères et demi-soeurs paternels des poissons de Glenariffe et entre les taux de survie des familles libérées des deux sites. La survie spécifique à la famille est en corrélation positive avec la masse à la libération, mais il y a des corrélations génétiques sous-jacentes qui ne s'expliquent pas par la taille. Dans leur ensemble, nos résultats laissent croire qu'il y a une influence génétique considérable sur la survie et le retour des saumons et que des adaptations spécifiques aux populations peuvent se développer en moins de 30 générations après leur établissement.

[Traduit par la Rédaction]

Introduction

One fundamental component of evolution is the differential probability of survival to reproductive age among individuals with different phenotypic traits. Such variation is observed not only within populations but also between populations, as different regimes of selection are associated with trait values. In fishes, for example, vulnerability to predation has been linked to patterns of morphology (Reimchen 1994), life history (Endler 1995), and behaviour (Magurran et al.

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1992). Salmonid fishes provide good opportunities to study natural selection because their life histories consist of distinct phases with associated agents of selective mortality. For example, fertilised eggs deposited in the gravel may suffer from poor water circulation associated with fine sediment (Chapman 1988) or gravel scour during floods (Thorne and Ames 1987), and juveniles in fresh water are lost to predation (e.g., Ruggerone and Rogers 1992). Salmonids appear to have adapted to these mortality agents by evolving a wide variety of population-specific traits, including egg size (Quinn et al. 1995), migratory behaviour (Brannon 1972), and morphology and aggression (Swain and Holtby 1989).

In addition to the agents of mortality in fresh water, anadromous salmonids face complex and poorly understood agents of mortality at sea. Within species, populations with larger migrants ("smolts") tend to experience higher survival rates than populations with smaller smolts (Koenings et al. 1993), though there is considerable variation in this regard. Within populations, survivors in a given year tend to be the larger smolts in a wide variety of salmonid species (e.g., chum salmon (*Oncorhynchus keta*), Healey 1982; coho salmon (*Oncorhynchus kisutch*), Holtby et al. 1990).

As well as the effects of body size, two lines of evidence suggest survival to adulthood is influenced by genetic factors. First, some families have higher rates of survival than other families of the same population (e.g., coho salmon (*O. kisutch*), McIntyre et al. 1988; pink salmon (*Oncorhynchus gorbuscha*), Geiger et al. 1997). Second, transplanted populations often have lower rates of survival or contribution to fisheries than local populations (e.g., Reisenbichler 1988). Survival reflects a suite of traits including size, foraging ability, feed conversion, and predator avoidance, so the genetic factors affecting it are likely to be complex. The importance of survival in determining how many progeny from any given mating contribute to future generations suggests that it should be heritable and thus amenable to natural selection. However, the patterns of selection may be complex, as biotic and abiotic factors causing differential survival may vary from year to year (e.g., Geiger et al. 1997).

Salmon populations were established in their native range by postglacial colonisation, followed by the evolution of population-specific traits that facilitated survival in that environment. The question is, how rapidly can a trait as complex as survival evolve? The successful translocation of chinook salmon (*Oncorhynchus tshawytscha*) from the Sacramento River, California, to the South Island of New Zealand (McDowall 1990) presented a unique opportunity to study the evolution and genetic control of survival to adulthood for several reasons. First, this represents the most long-standing and best understood case in which self-sustaining, anadromous populations of Pacific salmon have been established outside their native range. Second, the populations were established from a common source between 1901 and 1907 (Quinn et al. 2001) and have since diverged in a variety of phenotypic traits (Quinn and Unwin 1993; Unwin et al. 2000; Quinn et al. 2001). Third, there is no directed fishing for chinook salmon at sea, so returning adults represent virtually all fish surviving natural mortality. This permits a much more accurate estimate of survival than would be possible in North America, where both immature and maturing chinook are taken in the commercial fishery. Fourth, New Zealand chinook salmon populations are largely confined to the central east coast of the South Island, with their marine distribution apparently restricted to inshore waters along an 800-km coastline (Unwin and James 1998), so all populations inhabit rather more similar marine environments than their North American counterparts.

This study was designed to test the hypotheses that (*i*) New Zealand chinook salmon populations have diverged in traits that control survival, becoming adapted to their natal environment within a century of colonisation, and (*ii*) survival rates differ between families. We conducted experimental releases of tagged juvenile salmon from two populations, Glenariffe Stream and the Hakataramea River (Fig. 1), and two release locations (Glenariffe and Silverstream). Our null hypothesis was that survival (as measured by the rate of tag recovery for all returning adults) did not differ between populations or release locations. The predicted alternative, assuming adaptation to local conditions, was that Glenariffe fish would have higher survival rates when released from their home river. Environmental influences on survival could not be controlled, but releasing representatives of both populations at two locations and in two years allowed us to assess the extent to which survival rates depended on these two fixed factors. We then used return data for marked half-sib families to test the null hypothesis that survival would not vary among families. The predicted alternative was that some combination of smolt size and other family-specific attributes affected survival.

Materials and methods

Study populations and facilities

Glenariffe Stream is a stable, spring-fed stream joining the Rakaia River 100 km above the mouth at an altitude of 430 m (Fig. 1) and supports a mean annual spawning population of 1920 chinook (Unwin 1997). Spawning occurs from March to June (austral autumn), peaking in late April (Quinn and Unwin 1993). Wild juveniles leave the stream shortly after emergence from the redds (Unwin 1986) and rear in the mainstem Rakaia River for a few months or up to a year (Hopkins and Unwin 1987), entering the ocean in their first or second year of life (so-called ocean-type and stream-type chinook salmon, respectively). The Hakataramea River is a 60 km long rain-fed river joining the Waitaki River 60 km above the mouth at ~200 m elevation, 4 km below a dam blocking further upstream access to the Waitaki River (Fig. 1). As in Glenariffe Stream, Hakataramea River chinook salmon show a mixture of ocean- and stream-type juvenile life histories (Quinn and Unwin 1993).

Since 1980, naturally spawning stocks in Glenariffe Stream have been augmented by releases from a hatchery 200 m above the confluence with the Rakaia River (Unwin and Glova 1997). Yearling smolts released from this hatchery enter the upper Rakaia River and reach the South Pacific Ocean after a downstream migration thought to take only a few days (Unwin and Lucas 1993). The practice of releasing fall chinook as yearlings is unusual within their native range but became the norm in New Zealand following the widespread failure of earlier releases to achieve worthwhile returns (Unwin 1997). Hatchery yearlings are larger than their wild counterparts (Unwin and Lucas 1993) and tend to pro-

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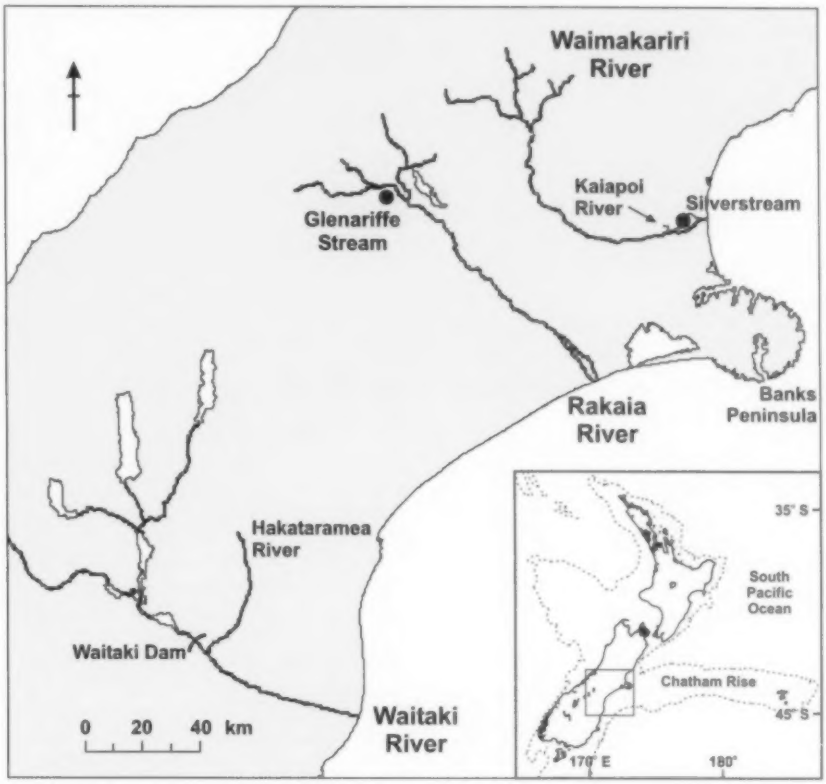
Fig. 1. The central South Island of New Zealand showing the source populations and release locations used in this study. The inset map shows the 1000-m isobath and the Chatham Rise to the east of the South Island.



duce higher returns of 2-year-old males (Unwin and Glova 1997) but appear similar to wild stocks in terms of annual variations in marine survival (Unwin 1997).

Experimental families from the Glenariffe (GA) and Hakataramea (Haka) populations were propagated in the Glenariffe Stream hatchery, which represented "home territory" for the GA fish. Representatives from these families were also reared in another hatchery on a third river system, the Silverstream Hatchery on the Kaiapoi River, a lowland tributary of the Waimakariri River, 13 km from the sea at an altitude of 17 m (Fig. 1). The Waimakariri River and its headwater tributaries support large chinook salmon populations, but the Kaiapoi River provides little natural spawning or juvenile rearing habitat and is populated only by fish of hatchery origin.

Establishment, culture, and release of experimental families

In 1994 we established 72 experimental families by spawning salmon from the two study populations on consecutive days (22 and 23 April for GA and Haka, respectively). We collected gametes from all available fish at each location but subsequently used scale pattern analysis (Unwin and Lucas 1993) to select parents that were almost exclusively age-3 ocean-type fish, and of natural rather than hatchery origin, to minimise variation among families in factors other than population of origin. We used milt from each male to fertilise ova from two randomly selected females in a half-sib mating design, creating 32 full-sib families nested within 16 half-sib families for the Haka population, and 40 full-sib families nested within 20 half-sib families for the GA population. All ova (~5000 per female) were taken from GA fish, but only 2000 ova were taken from each Haka female.

All families were individually incubated and reared at Silverstream Hatchery, using ambient (mean 12.1°C) ground water. As incubation progressed we reduced the number of families to 60, comprising 30 full-sib families within 15 half-sib families per population, primarily by culling both families from half-sib pairs for which one or both parents were of hatchery origin, or which were affected by unusually poor fertilisation or survival rates (see Kinnison et al. (1998*a*) and Quinn et al. (2000) for further details on the breeding and rearing protocols).

After hatching and completion of yolk absorption in early August, 700 fry from each family were set aside for further experiments, and the rest were transferred to circular tanks, each with a capacity of 3000 L. Each GA family (~4000 fry) was held in a single tank but Haka fry (~1000 per family) were pooled and divided evenly between two tanks (a necessary consequence of the limited number of tanks available). All fry were fed to satiation with a standard dry diet. In October 1994 (austral spring), 6 months after fertilisation, these fry were marked with sequential coded-wire tags (CWTs) to either population level (Haka) or family level (GA). Fry were also marked externally by excision of the adipose fin to

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indicate the presence of the internal tag. The tagged fry were trucked to the Glenariffe Hatchery and pooled into a single large raceway for common rearing. On 19 July 1995 (after 9 months of additional rearing), they were released into the upper Rakaia River from Glenariffe Hatchery. A subsample of 600 fish (nominally 20 per family) was sacrificed one day before release for measurement of fork length and weight and recovery of CWTs, allowing mean weight at release to be determined for each GA family and for the Haka population. Final release numbers were 117 824 GA fish (averaging 3927 per family at an average weight of 59 g) and 23 655 Haka fish at an average weight of 60 g. We refer to these fish as the 1994 Glenariffe release (where 1994 refers to the brood year rather than the year of release).

We established a second release group, representing 58 of the original 60 families, by accumulating surplus fish from the 700 set aside from each family in August 1994 (see Kinnison et al. (1998*b*) for further details). Fish from both populations were coded-wire tagged to family level after excision of the adipose fin, pooled in an external raceway, and released from Silverstream on 31 July 1995 (13 709 fish, averaging 232 (range 90–366) per family). These fish were the "1994 Silverstream release". Mean weight at release was 94 g for both populations but was not measured to family level because this would have required destructively sampling (for tag recovery) too many of the fish available for release. As a surrogate, we used mean weight (based on 50 fish per family) recorded on 14 May, 10 weeks before their release, in all calculations involving family-level comparisons of survival in relation to weight at release.

To protect against the possibility of a weak return from the 1994 brood year and to provide some degree of replication, we repeated the spawning programme in autumn 1995. We used a full-sib mating design to create 12 Haka and 13 GA families, following the same protocols for collecting gametes, incubating embryos, initial rearing at Silverstream, marking and tagging, and additional rearing at Glenariffe as for the 1994 brood year Glenariffe release group. On 29 July 1996, these fish were divided into two groups. The larger group (68 747 fish, averaging 2742 per family) remained at Glenariffe Hatchery, and the smaller group (15 753 fish, averaging 630 per family) was transferred back to Silverstream Hatchery. These two groups (the 1995 Glenariffe release and the 1995 Silverstream release) were released on 20 and 16 August 1996, respectively. We estimated the number of fish from each family released at each location by dividing the number of fish originally tagged in proportion to the total number of fish in each release group. Mean release weights at both locations, based on a sample of 500 fish sacrificed for tag recovery when the fish were divided into two groups, were 101 g (Haka) and 114 g (GA).

Tag recovery

Adult chinook from the Glenariffe and Silverstream release groups returned to fresh water at maturity in autumn 1996 to 1999, representing 2-, 3-, and 4-year-old fish from both the 1994 and 1995 broods. These fish were intercepted at the Glenariffe Stream and Silverstream counting fences and were also taken in the sports fishery as they ascended the Rakaia, Waimakariri, and other east coast rivers. The angler catch rate for both the Rakaia and Waimakariri rivers is typically 30–40% and varies little among years (Ross Millichamp, North Canterbury Fish and Game Council, Christchurch, New Zealand, personal communication), although tag recoveries from the sports fishery are typically underreported by about 50% (M.J. Unwin, unpublished data). We did not adjust the data to allow for unreported tags, so our survival estimates are conservative. However, they would be biased with respect to population of origin only if the probability of angler capture varied between populations. For the purposes of this study, we ignored this possibility. Tagged salmon taken incidentally at sea as a bycatch in commercial fisheries for other species accounted for 1.5% of the recoveries and were included in our survival estimates.

Heads from all salmon with a missing adipose fin were sent to the laboratory for tag recovery and identification. Because the 1995 Glenariffe and Silverstream release groups were established after the fish had been tagged, tag data did not uniquely establish the release location for each fish. We resolved this ambiguity by assuming (*i*) that all fish returning to either Glenariffe Stream or the Kaiapoi River were homing to their release site and (*ii*) that fish taken by anglers in all rivers except the lower Waimakariri River were of Glenariffe origin. This second assumption is consistent with very low straying rates for previous Silverstream releases (50 strays from 2916 returns (1.7%) over 20 years) compared with the higher straying rates (12%) of chinook released from Glenariffe Stream and also with the tendency for strays of GA origin to enter rivers to the north of the Rakaia (Unwin and Quinn 1993). Fish taken by anglers in the lower Waimakariri River below the Kaiapoi confluence (2% of the total recoveries) could have originated from either release site and were not used for calculating site-specific survival rates.

Data analysis

For pairwise comparisons between populations, release sites, and brood years, we calculated survival at population level (all families combined) as the ratio of tags recovered (n) to tags released (N), with confidence intervals based on the binomial distribution (Schnute 1992). Significance tests for comparisons between release groups were based on the z statistic. We also performed these comparisons using family-level survival data to provide a natural measure of within-population variability via the analysis of variance (ANOVA) model

$$(1) \qquad S_{ijkm} = \mu + O_j + Y_k + L_m + \text{interaction terms} + \varepsilon_{ijkm}$$

where O, Y, and L denote population of origin, year of release, and release location; S_{ijkm} denotes survival for family$_i$; and μ and ε represent mean and error terms, respectively. Family-specific survival rates were positively skewed, so we used a square-root transformation to improve normality, choosing this in preference to the more usual log-transformation (cf. Unwin 1997) because some families had zero survival at one or both release locations. Family-level survival estimates were not available for Haka fish in the 1994 Glenariffe release but the fish were released in two groups with separate tags, so we used survival data for those groups, which were

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reared in separate ponds before being tagged and thus represented independent replicates (cf. Schnute 1992), as surrogates. This model was used to combine both brood years and release locations in the same analysis.

Mean weight at release did not vary greatly between populations but differed between release locations and brood years. The lack of family-specific weight data on the day of release for some groups precluded an adjustment based on analysis of covariance, so we used the relationship between survival and mean release weight (W) for chinook salmon released from Glenariffe Hatchery between 1978 and 1990 (Unwin 1997) to adjust for differences in survival associated with variation in size. This result ($\log S \propto 1.34 \times \log W$) suggests a 2.5-fold increase in survival for each 2-fold increase in weight. We used this relationship to standardise population level survival rates to a common release weight, facilitating comparisons between release locations and brood years.

To characterise genetic influences on survival for the 1994 brood, we formulated our analysis in terms of probability of survival for the progeny of each family. We represented the N tagged fish in each family as a series of independent binomial trials, with the n tagged fish recovered as adults having a survival of 1 and the remaining $N - n$ having a survival of 0, via the model

$$(2) \qquad S_{ijk} = \mu + \text{sire}_i + \text{dam}_{j(i)} + \varepsilon_{ijk}$$

where sire and dam are treated as random effects. This formulation of the data implicitly allows for variation in the number of fish originally marked within each family. We estimated this model for the Glenariffe release (30 dams within 15 sires, all of Glenariffe origin) and the Silverstream release (58 dams within 29 sires), both with and without mean release weight (W) for each family as a covariate, to identify the extent to which genetic effects were associated with family-specific variation in release weight. We used restricted maximum likelihood (REML) procedures, as implemented in Genstat 5 (release 4.1; Genstat 5 Committee 1998), to estimate model 2 (eq. 2) with stepwise inclusion of sire, dam, and sire + dam effects, interpreting the incremental reduction in deviance ($-2 \times$ log-likelihood) as a χ^2 statistic with 1 df to evaluate the significance of each additional parameter. These analyses also estimated sire and dam variance components (and their associated sampling errors) for estimation of narrow-sense sire heritability (h^2) on the observed scale (Becker 1984; Lynch and Walsh 1998). Because heritabilities for characters represented by binomial data tend to be severely underestimated when frequencies (i.e., survival rates) differ significantly from 50%, we also converted these values into estimates of heritability on the underlying "liability scale" (Lynch and Walsh (1998), equation 25.8b). Standard errors for these estimates were based on the corresponding errors for the variance components.

We used a similar model to estimate family-level effects for the 1995 brood, with the addition of release location and population of origin, so as to allow for any effects related to population of origin (which was excluded from the 1994 analysis because family-specific data were not available at both release locations). However, with only full-sib families we were unable to differentiate between sire and dam effects. The model used was

$$(3) \qquad S_{ijkm} = \mu + O_i + \text{family}_{j(i)} + W_j + L_k + O_i \cdot L_k + \varepsilon_{ijkm}$$

using the same notation as model 1 (eq. 1) with the addition of family mean weight (W) as a covariate. We estimated this model for both release locations (Glenariffe and Silverstream) combined and also for each location separately after deleting all terms in L, using Wald tests (which approximate a χ^2 test, Genstat 5 Committee 1998) to determine the significance of fixed effects associated with population of origin and release location.

Results

Tag recoveries

A total of 1015 tags from 1994 and 1995 brood year chinook were recovered, of which 992 (97.7%) could be positively identified with respect to release location. Mean survival rates were 0.47 and 0.34% for the two brood years, respectively. Over 80% of the fish were recovered at the Glenariffe and Silverstream hatcheries; anglers took most of the rest. On the assumption that about half of the tagged chinook caught by anglers were reported, our data underestimated survival by between 0.05 and 0.1%. The number of tags recovered per family varied from an average of 15 (range 2 to 32) for the 1994 Glenariffe releases to 5 (range 0 to 14) for releases from Silverstream. Estimates of family-specific survival are therefore subject to considerable uncertainty, particularly for the 1994 Silverstream releases where (on average) each additional recovered tag represented an incremental change in survival of 0.4%.

As a check against the possibility that our population-specific estimates of survival might have been confounded by differential straying rates, we used tag returns for the 1994 Glenariffe release to compare straying rates for fish of GA and Haka origin. We detected no significant difference ($\chi^2 = 0.59$, $p > 0.25$), with straying rates of 11.9% (47 out of 395 recoveries), and 8.4% (4 out of 48 recoveries) for GA and Haka fish, respectively. Straying rates for the 1994 Silverstream release were too low to permit a statistically meaningful comparison (GA: 1 out of 130 recoveries; Haka: 2 out of 146 recoveries) but also suggested no marked difference between the two populations. We therefore assumed that any interpopulation differences in straying rates were too small to significantly bias our survival estimates.

Survival as a function of population and release location

Our initial analysis, including all salmon with tags indicating population of origin, showed that GA salmon had a significantly higher survival rate than Haka fish when released from Glenariffe but that survival rates for the two populations were similar when released from Silverstream (Table 1). Released from Glenariffe, the survival rate for GA fish was 1.7 times higher than for Haka fish in 1994 and 2.9 times higher in 1995. For the two brood years combined, mean survival rates were 0.33% for GA and 0.15% for Haka salmon. Released from Silverstream, Haka fish had a higher survival rate in 1994 and a lower survival rate in 1995 but in neither year was the difference between the two study populations significant (Table 1; $p > 0.1$ in both cases). Mean sur-

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Table 1. Estimated survival rates ± 1 standard error for 1994 and 1995 brood year chinook salmon of Glenariffe and Hakataramea origin released from the Glenariffe and Silverstream hatcheries, based on coded-wire tag recoveries.

Release location	Brood year	Population of origin	Mean weight (g)	Total released	Total returns	Survival, %	*p*
Glenariffe	1994	Glenariffe	59.1	117 824 (30)	402	0.34±0.02	<0.001
		Hakataramea	60.2	23 655 (2)	48	0.20±0.03	
	1995	Glenariffe	113.9	29 113 (13)	92	0.32±0.03	<0.001
		Hakataramea	101.1	39 634 (12)	42	0.11±0.02	
Silverstream	1994	Glenariffe	94.2	6 892 (29)	130	1.89±0.16	0.19
		Hakataramea		6 617 (29)	147	2.22±0.18	
	1995	Glenariffe	113.9	6 671 (13)	65	0.97±0.12	0.10
		Hakataramea	101.1	9 082 (12)	66	0.73±0.09	

Note: Numbers in parentheses, after the release totals, indicate the numbers of families or groups of families (1994 Hakataramea population) given discrete tags.

vival for the two brood years combined was 1.43% for GA and 1.47% for Haka fish.

More detailed analysis of the population-level difference, using model 1 with family-specific data, showed no significant two- or three-factor interactions ($p > 0.17$ in all cases) but significant effects associated with release location ($p << 0.001$) and brood year ($p = 0.02$). When analysed separately for each release location, there was no significant interaction between brood year and population of origin at either location ($p > 0.25$), indicating that population-level variation was consistent across brood years. For releases from Glenariffe, survival differed between populations ($p = 0.01$) but not between brood years ($p = 0.23$), whereas for releases from Silverstream, there was a strong brood year effect ($p = 0.004$) but no population effect ($p = 0.96$). Mean survival rates (transformed cell means ± 1 standard error (SE)) were 0.29 ± 0.03% for GA vs. 0.13 ± 0.04% for Haka families released from Glenariffe and 1.18 ± 0.19% for GA vs. 1.19 ± 0.20% for Haka families released from Silverstream. These results are consistent with those in Table 1, any differences being attributable to the effect of variation in the number of fish tagged within each family or release group (which influences the totals for N and n and the z statistics used to derive Table 1 but not the percentage survival figures used in the ANOVA).

The differences between the two study populations were not accounted for by differences in mean weight at release. For the 1994 releases, mean weights differed by little more than 1 g at either release location and at Glenariffe Stream should have favoured Haka fish (which were 1.1 g heavier). The more substantial differences in weight in 1995 were still insufficient to account for the observed differences in survival for releases from Glenariffe. When adjusted to a common release weight of 107 g (the mean for both populations), estimated survival rates for GA and Haka salmon were 0.31 and 0.12%, respectively, from Glenariffe Stream and 0.97 and 0.74%, respectively, from Silverstream.

Survival rates of chinook released from Silverstream were roughly 4-fold higher than for those released from Glenariffe Stream. Mean survival rates (± 1 SE) for the two release locations were 1.63% (1.49, 1.78) and 0.26% (0.12, 0.44), respectively, for the 1994 brood, and 0.81% (0.667, 0.97) and 0.17% (0.11, 0.25) for the 1995 brood. Adjusted to common release weights (60 g in 1994 and 107 g in 1995), survival rates for families released from Silverstream were approximately 6-fold higher than for releases from Glenariffe Stream in 1994 and 4-fold higher in 1995.

Family-level variation in survival

Survival varied considerably among families. For the 1994 brood, survival ranged from 0.04 to 0.89% for releases from Glenariffe Stream and from 0.0 to 5.8% for releases from Silverstream. Corresponding figures for the 1995 brood were 0.0 to 0.58% (Glenariffe releases) and 0.15 to 2.02% (Silverstream releases). As noted earlier, survival rates were positively skewed but tended to be more leptokurtic (with a higher proportion of extreme values) than would be expected had they been distributed randomly, in accordance with the Poisson (or gamma) distribution (Fig. 2). Within each brood year, family-specific survival rates were correlated between the two release locations (1994, $r^2 = 0.19$, $p = 0.02$; 1995, $r^2 = 0.22$, $p = 0.02$; Fig. 3). Family-specific survival was correlated with weight at release for the 1995 releases (Glenariffe, $r^2 = 0.36$, $N = 25$, $p = 0.001$; Silverstream, $r^2 = 0.20$, $N = 25$, $p = 0.03$) but not for the 1994 releases from either site (Glenariffe, $r^2 = 0.09$, $N = 30$, $p = 0.1$; Silverstream, $r^2 = 0.04$, $N = 58$, $p = 0.15$; Fig. 4).

Sire or dam effects on survival were apparent for all 1994 brood release groups, but the nature of these effects varied strikingly between release locations (Table 2). For releases from Glenariffe Stream, sire effects were highly significant ($\chi^2 \geq 68.8$, df = 1, $p << 0.001$), whereas dam effects were not detectable ($p \geq 0.11$; Fig. 5*a*). By contrast, dam effects were significant at Silverstream ($\chi^2 \geq 33.2$, df = 1, $p << 0.001$), whereas no sire effect was detected ($p \geq 0.79$; Fig. 5*b*). These results were unchanged when mean family weight at release was included as a covariate, confirming that the observed effects were independent of any family-specific variation in weight. In accordance with the observed sire effects, sire heritability was small ($h^2 \approx 0.004$ on the observed scale, $h^2 \approx 0.12$ on liability scale) but significantly greater than zero for the 1994 Glenariffe releases but did not differ significantly from zero for the Silverstream releases. As with the significance tests listed in Table 2, these heritability estimates were essentially unaffected when the model was adjusted to allow for interfamily variation in release weight.

For the 1995 brood year, the results of model 3 for both release sites combined also showed significant interfamily variation (Table 2) and a strong effect associated with release location ($p << 0.001$). When analysed separately for

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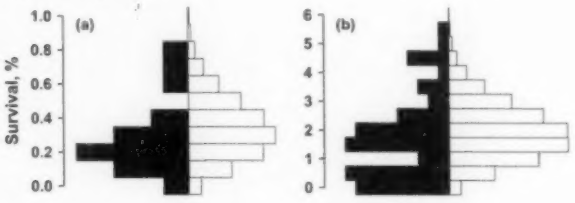
Fig. 2. Observed distribution of family-specific survival rates (%) for chinook salmon (*Oncorhynchus tshawytscha*) released from (*a*) Glenariffe Stream ($N = 32$) and (*b*) Silverstream ($N = 58$) in 1994, together with the expected frequencies for a Poisson distribution with the same mean survival. Observed, solid bars; expected, open bars.



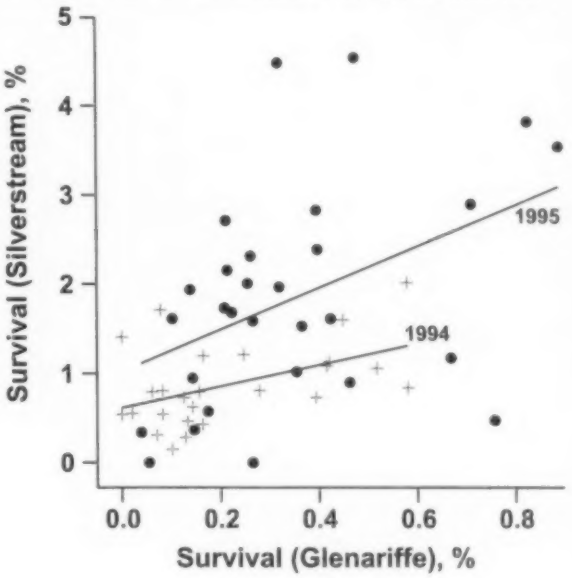
each release location, interfamily effects were apparent for the Glenariffe Stream releases but not for the Silverstream releases (Table 2). Likewise, population of origin effects were marginally significant at Glenariffe ($p \approx 0.05$) but not at Silverstream ($p \approx 0.99$).

Discussion

Our results provided strong experimental evidence that variation in survival of chinook salmon was associated with genetic variation at both family and population level. First, in two consecutive release years, GA salmon had higher survival than Haka fish only when released from their native stream. This supports the hypothesis that GA fish have adapted in ways that increase their survival in Glenariffe Stream, the Rakaia River, and the local marine environment relative to salmon from another river. Although the differences in survival between GA and Haka fish were small in absolute terms (a few parts in 10^{-3}), they represented a 1.5- to 3-fold difference in survival rate and hence in the mean number of recruits per spawner. Second, the presence of a strong sire effect on survival rates for half-sib families released from Glenariffe Stream, beyond any effects associated with weight at release, and an equally marked dam effect for releases from Silverstream supported the hypothesis that survival is controlled by family-specific traits as well as by size. The correlation of family-specific survival rates between sites also indicated underlying genetic control, despite the environmental effect revealed by the higher survival of fish released from Silverstream.

This study was part of a large research programme on New Zealand chinook salmon with the primary goal of determining whether they have evolved into genetically distinct populations since their establishment in the early 1900s (Quinn and Unwin 1993; Quinn et al. 2001). The apparent "home-court" advantage of GA over Haka fish at Glenariffe Stream but their similar performance on "neutral territory" suggests that some degree of interpopulation genetic differentiation has occurred in less than 100 years (~30 generations). We also have evidence of genetically controlled differences in juvenile growth rate (Kinnison et al. 1998*a*; Unwin et al. 2000), the timing of adult return migration and spawning (Quinn et al. 2000), and reproductive allocation in females (Kinnison et al. 2001). Logistic considerations prevented us from performing a more complete experimental test of our primary hypothesis by releasing tagged fish from both study

Fig. 3. Family-specific survival rates (%) for 53 families of chinook salmon (*Oncorhynchus tshawytscha*) released from Glenariffe Stream and Silverstream in 1994 (+) and 1995 (●).



populations into the Hakataramea River, but our results invite the prediction that Haka fish would have outperformed those of GA at that location.

There is no way of knowing what properties or traits the GA-origin fish possessed that conferred the higher survival rate (relative to Haka River fish) when released from the upper Rakaia River but were nullified when released from Silverstream, in the lower reaches of the Waimakariri River. Size affected survival at the family level but did not explain the population effects. Factors influencing marine survival and mortality of salmon are poorly understood, especially in a non-native environment such as the South Pacific Ocean, but behaviour may have played a role. There is considerable evidence for genetic control over behaviour in fishes (Trexler 1990) and in salmonids in particular, including such traits that might influence survival as aggression (Rosenau and McPhail 1987; Swain and Holtby 1989), schooling (Swain and Holtby 1989), and predator avoidance (Johnsson and Abrahams 1991).

The conclusion that survival was influenced by genetic factors was supported by the tendency for survival rates for individual families to be correlated at both release sites and for offspring sired by the same males to have similar survival rates. Family-specific survival rates were positively correlated with mean weight at release. This is consistent with other studies showing that larger individuals in a given cohort are more likely to survive than smaller ones (e.g., Healey 1982; Holtby et al. 1990; Henderson and Cass 1991), though the earlier studies did not have family-specific data. The relationship between weight (a trait under genetic influence) and survival in itself thus represents an indirect but clear genetic influence on survival. However, analysis of sire and dam effects indicated that weight at release was insufficient to account for the observed differences in survival among families.

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Fig. 4. Family-specific survival (%) vs. mean weight at release (g) for chinook salmon (*Oncorhynchus tshawytscha*) released as yearlings from Glenariffe Stream in 1994 (*a*) and 1995 (*b*) and Silverstream in 1994 (*c*) and 1995 (*d*).

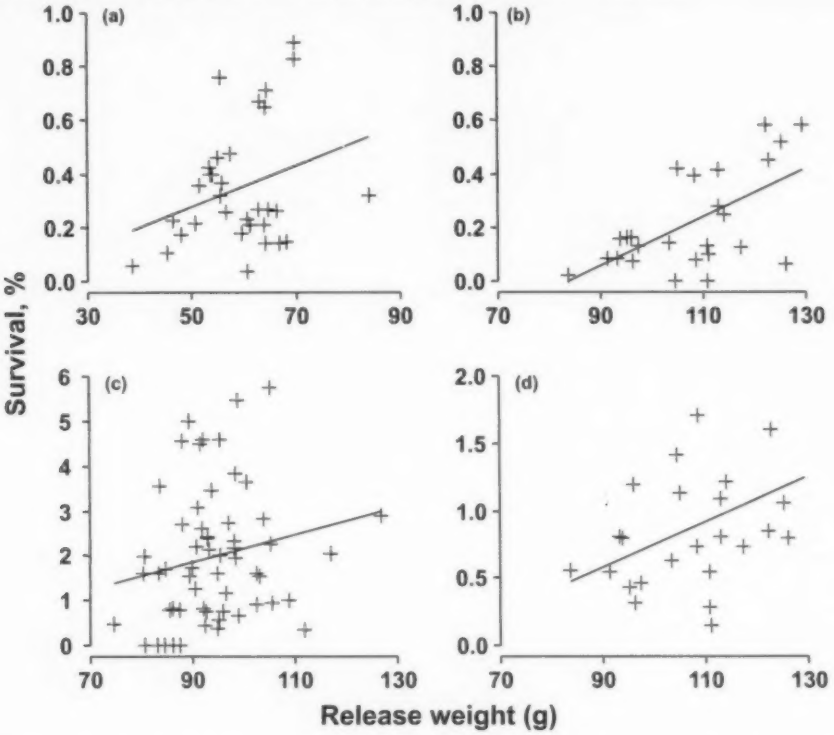

Table 2. Significance of sire, dam, or family effects on marine survival of 1994 and 1995 brood year chinook salmon released from Glenariffe and Silverstream, based on restricted maximum likelihood analysis of linear mixed models (performed separately for each brood year), together with sire heritability estimates for the 1994 brood ($h^2 \pm 1$ standard error) on both the observed and liability scales.

						h^2	
Brood year	Release location	Sample size *N*, sires (dams)	Effect	Weight as covariate	*p*	Observed scale	Liability scale
1994	Glenariffe	117 824, 30 (15)	Sire	No	<0.001	0.004±0.002	0.12±0.06
			Sire	Yes	<0.001	0.004±0.002	0.12±0.06
			Dam	No	0.11		
			Dam	Yes	0.21		
1994	Silverstream	13 509, 58 (29)	Sire	No	0.79	0.008±0.013	0.07±0.10
			Sire	Yes	0.92	0.002±0.010	0.02±0.08
			Dam	No	<0.001		
			Dam	Yes	<0.001		
1995	Combined	84 500, 25 (25)	Family	Yes	0.002		
	Glenariffe	68 747, 25 (25)	Family	Yes	0.003		
	Silverstream	15 753, 25 (25)	Family	Yes	0.70		

Note: Models that included weight at release as a covariate are indicated.

Salinity tolerance is correlated with size in salmon smolts, and this might contribute to the variation in survival among families. We compared survival rates for the 1994 brood year fish from this experiment with the results of salinity-tolerance experiments (described in detail in Kinnison et al. 1998*a*) conducted on the same families on two occasions, November 1994 and May 1995. Salinity tolerance was correlated with body size (Kinnison et al. 1998*a*) but survival showed little consistent relationship to salinity tolerance at either challenge date. For families released from Glenariffe, survival was weakly correlated with salinity tolerance when measured in November 1994 ($r = 0.37$, $p = 0.055$) but not when measured in May 1995 ($r = 0.17$, $p = 0.54$). For the Silverstream releases, survival was uncorrelated with salinity tolerance at either experimental period.

Although genetic control over survival was significant, estimated sire heritabilities ($h^2 \leq 0.12$ on the liability scale) were not particularly high compared with values approach-

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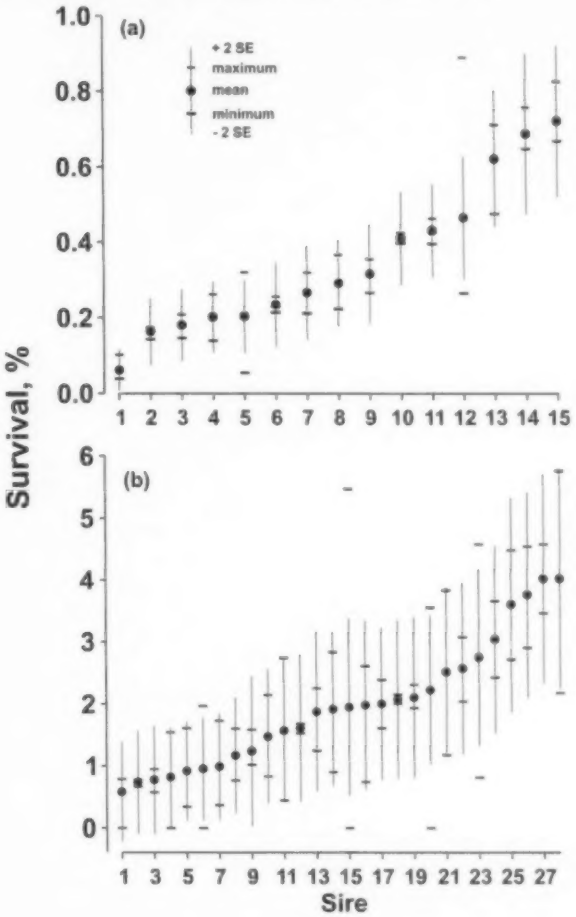
Fig. 5. Marine survival (%) for half-sib families of 1994 brood year chinook salmon (*Oncorhynchus tshawytscha*) released from (*a*) Glenariffe Stream (30 families) and (*b*) Silverstream (58 families). Sires have been ordered to emphasise variation between families within sires (–) relative to variation between sires (●). Error bars are based on returns for each sire averaged across both families. Note the low within-sire variation at Glenariffe compared with the high variation at Silverstream. SE, standard error.



ing 1.0 for the timing of adult return and maturation (Quinn et al. 2000) and values of about 0.7 for egg size, fecundity, and ovary mass (Kinnison et al. 2001) calculated for the same families. Timing and egg production are more discrete traits, whereas survival is the resultant of a number of traits, which may strike a different balance within and between families. Traits more closely related to fitness may have lower heritability than traits less correlated with fitness in laboratory (Roff and Mousseau 1987) and wild populations (Kruuk et al. 2000; Merila and Sheldon 2000). Lower calculated heritability may result from little additive genetic variation or considerable residual (environmental or dominance) variation. This latter hypothesis is supported by the work of Merila and Sheldon (2000) and Kruuk et al. (2000) using the coefficient of additive genetic variation rather than heritability. Survival in the ocean is likely to have great environmental variation so this seems a plausible explanation for the low heritability in our data.

One indication of environmental control over survival was the markedly higher survival for sibling chinook from both study populations when released from Silverstream compared with Glenariffe. Mean release weights at the two locations were either the same (in 1995) or not large enough to account for the difference in survival (1994). Our results do not allow us to differentiate between freshwater and marine influences on survival, both of which may have contributed to the observed differences between the two release locations. Within the freshwater environment, the longer downstream migration path to the sea from Glenariffe Stream, relative to Silverstream (100 vs. 13 km), may have contributed to higher mortality rates before seawater entry. Yearling hatchery chinook released from Glenariffe Stream appear to reach the mouth of the Rakaia River within a few days (Unwin and Lucas 1993), so it is unlikely that differential mortality during this period was the primary reason for the observed differences between the two release locations. However, it is also possible that at the adult end of the life cycle, differences in the cost of upriver migration may affect survival between release sites and populations. Chinook released from Silverstream undertake a much shorter freshwater return migration than their Glenariffe counterparts, which also must gain an altitude of 430 m. These differences impose significant costs on energy reserves and reproductive investment (Kinnison et al. 2001) and could potentially affect survival.

Within the marine environment off the east coast of the South Island, numerous factors (e.g. predators, prey abundance, or ocean currents) potentially affecting survival could differ between the mouths of the two rivers or the larger regions occupied by the salmon as they grow to maturity. The migratory movements of New Zealand salmon at sea are poorly known, although there is some evidence that individual populations have a relatively localised marine distribution, particularly when compared with North American populations (Unwin and James 1998). Coded-wire tag recoveries show that salmon of Rakaia origin commonly stray to rivers north of Banks Peninsula (Unwin and Quinn 1993) but (as noted earlier) that salmon released into the Waimakariri River are only rarely recovered south of this point, suggesting that their respective marine distributions overlap but do not coincide. Differences in the marine environment off these two rivers may be further accentuated by the presence of the Chatham Rise, a prominent undersea ridge east of Banks Peninsula associated with marked north–south gradients in water temperature and salinity (Unwin and James (1998) and references therein). Survival rates for fish released from Glenariffe and Silverstream over the last two decades have tended to be no more than weakly correlated (M.J. Unwin, unpublished data), with higher survival rates for Glenariffe releases during the early to mid-1980s but higher survival for Silverstream releases in the late 1980s and early 1990s.

The implications of this study are that not only does marine survival have a substantial genetic component (through smolt size and less obvious additional mechanisms) among families, but also that population-specific differences can evolve in the comparatively short time frame of about 30 generations. This rapid evolution is particularly striking given the fact that the

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New Zealand rivers all discharge into the South Pacific Ocean over a limited (~200 km) length of coastline and that the major salmon-producing rivers (including those in this study) have broadly similar physical characteristics. All lack major estuaries, are comparatively short and steep, flow through broad, gravel-rich braided channels, lack significant tributaries in the middle and lower reaches, and tend to flood in an erratic but synchronous pattern among rivers. We infer that despite these similarities, environmental conditions experienced by their chinook salmon are sufficiently different, and the traits sufficiently heritable, to give rise to locally adapted populations in this brief period of time. This not only presents a window into the rapid evolution of Pacific salmon, but also may provide encouragement to efforts to restore extirpated populations within their native range. Although such efforts will be fraught with difficulties, it is important to know that salmon display considerable scope for evolution.

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The importance of dietary phosphorus and highly unsaturated fatty acids for sockeye (*Oncorhynchus nerka*) growth in Lake Washington — a bioenergetics approach

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Abstract: Juvenile sockeye salmon (*Oncorhynchus nerka*) in Lake Washington experience very high growth rates, but the mechanisms regulating their growth rates are poorly understood. The potential for food quality limitation of growth was tested using a coupled bioenergetics and mass balance model. Sockeye and zooplankton prey species were analyzed for their fatty acid composition. Ratios of phosphorus to carbon (P:C) for both sockeye and zooplankton were obtained from the literature. Based on sockeye stomach contents and zooplankton weights, diets of zooplankton biomass were calculated and monthly values of specific fatty acids and P:C ratios in the diet were derived. An increase in highly unsaturated fatty acids, especially in the liver, was observed with increased fork length up to smoltification size, with a subsequent decrease in smolts and kokanee. Measurements of docosahexaenoic (DHA) in daphnids were significantly lower than in cyclopoids. Model predictions suggest that sockeye are not limited by the availability of phosphorus or eicosapentaeinoic acid (EPA) in their diet but may experience limited growth because of DHA deficiencies. Thus, the ability and efficiency of sockeye at elongating 18:3 ω3, 18:4 ω3, and EPA to DHA may be of critical importance to lacustrine growth and production.

Résumé : Les jeunes saumons rouges (*Oncorhynchus nerka*) du lac Washington ont des taux de croissance très élevés, mais les mécanismes qui contrôlent ces taux restent mal connus. Nous avons évalué la possibilité d'une limitation de la croissance par la qualité de la nourriture en couplant une étude énergétique et un modèle de bilan de masse. La composition en acides gras a été déterminée chez les saumons et leurs proies dans le zooplancton. Les rapports phosphore:carbone (P:C) du saumon et du zooplancton ont été tirés de la littérature. L'étude des contenus stomacaux des saumons et de la masse du zooplancton nous a permis de calculer la biomasse du zooplancton dans le régime alimentaire et d'obtenir les mesures mensuelles des acides gras spécifiques et du rapport P:C dans le régime. On observe une augmentation des acides gras hautement insaturés, particulièrement dans le foie, à mesure de l'accroissement de la longueur à la fourche jusqu'à la taille de la transformation en saumoneaux; ces acides gras diminuent ensuite chez les saumoneaux et les kokanis. Les concentrations d'acide docosahexanoïque (DHA) sont significativement plus basses chez les daphnies que chez les cyclopoïdes. Les prédictions du modèle font croire que les saumons rouges ne sont pas limités par la disponibilité du phosphore ou de l'acide eicosapentanoïque (EPA) dans leur régime, mais que leur croissance peut être restreinte par manque de DHA. Ainsi, la capacité et l'efficacité du saumon rouge à allonger les acides gras 18:3 ω3, 18:4 ω3 et l'EPA en DHA peuvent être des facteurs déterminants de la croissance et de la production dans le lac.

[Traduit par la Rédaction]

Introduction

The constraints imposed on the growth of organisms by the availability of resources have long been the focus of study in ecology (Tilman 1982). Researchers investigating factors governing consumer growth (Gulati and DeMott 1997) have revitalized this focus of research in the aquatic sciences. However, almost all research in ecology that has been conducted on food quality has focused on the phytoplankton–zooplankton interface. Few studies have attempted to apply principles describing lower-trophic level processes to subsequent higher-trophic level consumers, such as fish (Nakashima and Leggett

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1980; Kraft 1992). Results from bioenergetics analyses of several freshwater fish populations feeding on a variety of prey revealed that all fish considered grew below optimal levels, but more interestingly, their growth was never predicted to be limited by nitrogen (N) and seldom limited by phosphorus (P) (Schindler and Eby 1997). A study of fatty acid composition among various fish species from lakes of differing trophic state found higher ω3 fatty acid content in fish sampled from relatively oligotrophic lakes with phytoplankton assemblages dominated by diatoms rich in ω3 fatty acids (Ahlgren et al. 1996). However, the potential for growth limitation because of essential fatty acid content has never been explored using bioenergetics models.

There is a wealth of knowledge on nutritional physiology of fish with respect to fatty acids in the aquaculture literature. For example, Yu and Sinnhuber (1979) fed coho salmon (*Oncorhynchus kisutch*) artificial feeds with varying fatty acid content and found that the optimal dietary ω3 fatty acid content for maximum growth was between 1 and 2.5% dry weight. Coho consuming diets containing a percentage of ω3 fatty acids beyond this range experienced reduced growth. Higher growth rates have been observed in rainbow trout (*Oncorhynchus mykiss*) and chum salmon (*Oncorhynchus keta*) when supplied with diets rich in the long-chained ω3 fatty acids eicosapentaenoic acid (20:5 ω3 or EPA) and docosahexaenoic acid (22:6 ω3 or DHA) (Takeguchi and Watanabe 1982). EPA and DHA, collectively referred to as highly unsaturated fatty acids (HUFA), are important nutrients for salmonid growth. Physiological studies have revealed that ω3 fatty acids are required for proper development of eye and brain tissue within developing rainbow trout (Bell and Tocher 1989). However, few studies have examined wild salmonid populations feeding on natural diets.

Sockeye salmon (*Oncorhynchus nerka*) were selected as the subject of this study for several reasons. First, they have high concentrations of ω3 fatty acids (Higgs et al. 1995) and it has been suggested that they may in some systems experience phosphorus-limited growth (Schindler and Eby 1997). Second, they have evolved a unique "adfluvial" life history, whereby young fry remain in nursery lakes to develop for 1–2 years before seaward migration, which greatly facilitates studies of their early development. However, the growth rates and residence times in these lakes vary tremendously; individuals that grow quickly leave the lake after only 1 year, whereas others grow more slowly and remain in the lake for 2 years (Weatherley and Gill 1995). Finally, according to Eggers (1982), sockeye in Lake Washington are obligate planktivores and feed almost exclusively on zooplankton throughout their lacustrine development, which greatly simplifies the analysis of prey items in their diet.

Extensive research has been conducted on the sockeye populations of Lake Washington (Woodey 1972; Beauchamp et al. 1989). Sockeye were first introduced to the Lake Washington system in 1935 and have proliferated since the 1960s (Edmondson 1994). Lake Washington is renowned for producing large sockeye smolts relative to other nursery lakes and the early departure of these smolts after only 1 year (Eggers 1978). The explanation provided by Eggers (1978) is that "the large size achieved by Lake Washington sockeye is due to a long growing season as well as a high rate of growth". Although this describes the proximate mechanisms, it fails to describe the ultimate nutritional and physiological factors that may enhance or restrict sockeye growth in Lake Washington.

The purpose of this research is to test the hypothesis that sockeye salmon in Lake Washington experience growth limitation because of content of phosphorus or specific essential fatty acids in their diet. A permutation of the basic mass balance model as proposed by Nakashima and Leggett (1980) was coupled with a bioenergetics model for sockeye (Beauchamp et al. 1989) to explore the possibility that sockeye experience limited growth resulting from dietary constraints. This analysis will assess the degree to which food quality, in terms of phosphorus, EPA, and DHA, limit sockeye growth in Lake Washington.

Materials and methods

Field sampling

Samples for both zooplankton and sockeye were collected concurrently from Lake Washington throughout the April 1999 to September 1999 growth season. Zooplankton were sampled from 0- to 20-m depth using a 250-μm zooplankton net. Zooplankton taxa were identified to genus and enumerated. Lake Washington has five *Daphnia* species (*D. ambigua*, *D. galeata*, *D. thorata*, *D. schodleri*, and *D. pulicaria*), of which *D. pulicaria* is the most abundant. *Daphnia* spp. were only distinguished to genus as they vary little in size and have similar feeding behaviors and elemental composition (Hessen and Lyche 1991; Brett et al. 2000). *Daphnia* spp. were, however, separated based on the presence or absence of eggs and were analyzed separately. The other prey taxa collected were *Cyclops* spp., which consisted of two species (*C. bicuspidatus* and *C. vernalis*) with the former being the dominant, as well as *Epischura nevadensis* and *Diaptomus ashlandi*. Other prey taxa such as the pelagic *Bosmina longirostris* and the benthic *Neomysis mercedis* were present at such low levels in zooplankton tows that they probably constitute a small portion of the sockeye diet in Lake Washington. Furthermore, of 688 juvenile sockeye salmon stomach samples collected, only three contained *Neomysis mercedis*, thus *Neomysis mercedis* constitute less than 1% of the sockeye diet (Jennifer Anson, Department of Zoology, University of Washington, Seattle, WA 98195, U.S.A., unpublished data). Eggers (1982) identified six zooplankton taxa in the diet of Lake Washington sockeye: *Cyclops*, *Diaptomus*, *Bosmina*, *Diaphanosoma*, *Epischura*, and *Daphnia*. Ivlev electivity indices

$$E_i = (r_i - p_i)/(r_i + p_i)$$

were calculated based on Eggers' (1982) data, where r_i is the percent of prey in the diet and p_i is the percent of prey in the environment. The proliferation of *Daphnia* in Lake Washington, which occurred in 1976 (Edmondson 1994), coincided with a decline in *Diaphanasoma*. Thus, *Diaphanasoma* is probably less important in the diet of sockeye today and was excluded from further analysis. Subsequently, *Daphnia* constitute an even greater proportion of the sockeye diet today as inferred from stomach content data. Sockeye were collected at night using a beach seine. Fork length was measured and flesh samples were taken from dorsal muscle and liver tissue.

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All samples were freeze-dried and weighed, and an internal standard of 21:0 was added, as this fatty acid is not commonly found in nature. They were then sonicated, extracted three consecutive times, and methylated (Kattner and Fricke 1986) before injection into a gas chromatograph (HP6890) equipped with a programmable temperature vaporizer-injector (PTV) for measuring samples of low concentration. A fused silica DB-WAX capillary column, manufactured by J&W Scientific (Folsom, Calif.), with a length of 30 m, a diameter of 320 μm, and a thickness of 0.25 μm was installed. Injected samples were subject to the following oven temperature regime: 5 min at 40°C, then heated to 150°C at a rate of 10°C/min, then kept at 150°C for 5 min, further heated to 220°C at a rate of 2°C/min, and finally kept at 220°C for 20 min. Sample peaks were detected using a flame ionization detector. Retention times were verified with a quantitative mixture of fatty acids (No. 625024, Alltech, Australia) and area curves compared between standards and samples for 18:3 ω3, EPA, and DHA showed less than 5% variability.

An analysis of variance (ANOVA) was conducted on fatty acid concentrations among the prey genera followed by a Tukey test to identify significant differences between prey types.

Bioenergetics modeling

The basic mass balance model as it applies to food quality includes parameters describing growth (G_Q), consumption (C_Q), egestion (E_Q), and excretion (U_Q), where Q represents the food quality parameter (i.e., phosphorus or fatty acids) and is expressed accordingly:

$$(1) \quad G_Q = C_Q - E_Q - U_Q$$

However, as fatty acids can be readily converted to triacylglycerols and stored as a major fuel source (Stryer 1981), they are probably not excreted but rather metabolized. Thus, essential fatty acids are first incorporated into growing tissues and then, if supplied in excess, are utilized as an energy source. The mass of fatty acids that can be metabolized (M_Q) in fish can then be written as

$$(2) \quad M_Q = C_Q - G_Q - E_Q$$

The mass of consumed fatty acids or phosphorus that are assimilated can be written as $C_Q \cdot AE_Q$, where AE represents the assimilation efficiency. The assimilation efficiency of 0.93 (Bell and Sargent 1992) for polyunsaturated fatty acids in a similar salmonid (*O. keta*) was used as an estimate of AE for sockeye. The average assimilation efficiency for phosphorus of 0.74 (±0.06) (Nakashima and Leggett 1980) was used because it represents the potentially limiting element to sockeye growth, based on the stoichiometric relationship between carbon and phosphorus in their diet. Thus, eq. 2 can be rewritten as

$$(3) \quad M_Q = (AE_Q \cdot C_Q) - G_Q$$

Therefore by solving eq. 3 for M_Q we can calculate the amount of surplus fatty acids that may be allocated to energy stores and predict whether growth limitation is experienced when feeding on an actual diet of varying prey types. Likewise, eq. 3 can be evaluated for the possibility of growth limitation resulting from the relative availability of phosphorus to carbon (P:C). Thus, a fish with a high P:C ratio could experience phosphorus-limited growth on a diet with a relatively low P:C ratio. This suggests that as the term for food that can be metabolized (M_Q) approaches zero with increased specific growth rate, surplus fatty acids or phosphorus are reduced, resulting in growth limitation. The main assumption of this model is the conservation of mass, meaning that fatty acids and phosphorus do not change following consumption. Although ω3 fatty acids cannot be synthesized by fish de novo and are thus considered to be essential, there is evidence that certain species can elongate 18 carbon chain ω3 fatty acids after consumption (Buzzi et al. 1996; Ruyter et al. 2000*a*). However, the actual rates and metabolic costs of elongation have not yet been measured in salmonids.

Because of the allometric (Peters 1983) and thermal scaling of metabolism (Weatherley and Gill 1995), the mass balance model (eq. 3) must be coupled to a bioenergetics model to evaluate changes in consumption and metabolism at various growth rates and thermal regimes. The original bioenergetics model refined by Hewett and Johnson (1991) and later used in concert with mass balance equations (Kraft 1992) is as follows:

$$(4) \quad \text{Consump} = \text{Growth} + \text{Resp}_{\text{standard}} + \text{Resp}_{\text{activity}} + \text{Resp}_{\text{digestion}} + \text{Egestion}_{\text{fecal}} + \text{Excretion}_{\text{urine}}$$

This bioenergetics model can be distinguished from the original mass balance equation (eq. 1) by the presence of the respiration terms for standard, activity, and digestion, which are strongly influenced by temperature. The other important distinction is that this model functions in units of energy (J) as opposed to the mass balance equations (eqs. 1–3), which function in units of mass (g·g wet weight (wet wt.)$^{-1}$). Specific equations and parameter values for the sockeye bioenergetics model can be found in Table 1.

Energy densities (J·g wet wt.$^{-1}$) for all prey species and sockeye were also required as inputs to the model, along with measurements of fatty acid content and P:C ratios for each of the prey species (Table 2). Stomach contents for Lake Washington sockeye were collected during the day and night at monthly intervals for the period 1994–1998 (Jennifer Anson, Department of Zoology, University of Washington, Seattle, WA 98195, U.S.A., unpublished data). Stomach contents were identified to genus and enumerated. From these data, monthly averages of zooplankton consumed were converted to biomass, based on zooplankton weights averaged over the sockeye growing season. Finally, monthly weighted averages for P:C ratios, EPA, DHA, and energy density were calculated and input to the model. It is also important to mention that the model, through a series of algorithms, fits a growth curve based on the energy density of the prey. The trajectory of this growth curve is reflected in P_{max}, or the proportion of maximum consumption, based on temperature and the initial and final wet weights of the fish. Thus, by maximizing consumption (i.e., $P_{max} = 1.0$), maximum growth rates were predicted for comparison with observed growth rates. Moreover, all dietary parameter inputs to the model are in terms of wet weight because measurements of fish biomass are in wet weight.

Data on sockeye growth in Lake Washington were obtained from Woodey (1972) and these data were corroborated by

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Table 1. Equations and parameter values for the bioenergetics model obtained from Beauchamp et al. (1989) and references therein.

Equations and parameters	Description and units	Values
Consumption (*C*)		
$C = C_{max}P_{max}f(T)$		
$f(T) = K_A - K_B$		
where		
$K_A = (CK1 \cdot L1)/(1 + CK1(L1 - 1))$		
$L1 = e^{(G1(T - CQ))}$		
$G1 = (1/(CTO - CQ)) \cdot \ln((0.98(1 - CK1))/(CK1 \cdot 0.02))$		
$K_B = (CK4 \cdot L2)/(1 + CK4(L2 - 1))$		
$L2 = e^{(G2(CTL - T))}$		
$G2 = (1/(CTL - CTO)) \cdot \ln((0.98(1 - CK4))/(CK4 \cdot 0.02))$		
CA	Intercept: mass dependence of maximum consumption (C_{max}) ($g \cdot g^{-1} \cdot day^{-1}$)	0.303
CB	Coefficient: mass dependence of C_{max}	–0.275
CQ	Temperature for CK1 (°C)	3
CTO	Optimum temperature for C_{max} (°C)	20
CTL	Temperature for CK4 (°C)	24
CK1	Proportion of C_{max} at temperature CQ	0.58
CK4	Proportion of C_{max} at temperature CTL	0.5
Respiration (*R*)		
$R = RA \cdot W^{RB*} f(T) \cdot ACT$		
$f(T) = e^{(RQ \cdot T)}$ and $ACT = e^{(RTO \cdot VEL)}$		
$VEL = W^{RK4}$		
$S = SDA(C - E)$		
RA	Intercept: R ($g\ O_2 \cdot day^{-1}$)	0.00143
RB	Coefficient: mass dependence of R	–0.209
RQ	Coefficient: R with respect to temperature	0.086
RTO	Coefficient: R with respect to swimming speed (U)	0.0234
ACT	Intercept: U ($cm \cdot s^{-1}$)	9.9
RK4	Coefficient: mass dependence of U	0.13
BACT	Coefficient: U with respect to temperature	0.0405
SDA	Specific dynamic action	0.172
S	Proportion of energy lost to SDA	
W	Fish mass (g)	Monthly values (see Fig. 1)
Egestion (*E*)		
$E = PF \cdot C$		
$PF = ((PE - 0.1)/0.9)$		
$PE = EA \cdot T^{EB} \cdot e^{EG}$		
EA	Intercept: proportion egested	0.212
EB	Coefficient: E with respect to temperature	–0.222
EG	Coefficient: proportion of maximum consumption (P_{max}) with respect to E	0.631
Excretion (*U*)		
$U = UA \cdot T^{UB} \cdot e^{UG}(C - E)$		
UA	Intercept: proportion excreted	0.0314
UB	Coefficient: U with respect to temperature	0.58
UG	Coefficient: P_{max} with respect to U	–0.299

more recent observations (T. Quinn, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, U.S.A., unpublished data) (Fig. 1). Initial and final weights for each month were then used as inputs to the model. Specific growth rates (g) were also calculated for each month interval according to eq. 5 for comparison with predicted growth rates:

$$(5) \qquad g = [\ln(W_t) - \ln(W_i)]/t$$

where W_i represents the initial weight, W_t the final weight, and t is the length of each month in days.

Temperature regimes were obtained for 20-m depth (D.E. Schindler, Department of Zoology, University of Washington, Seattle, WA 98195, U.S.A., unpublished data) and input to the model. The depth of 20 m was decided on as an intermediate depth between sockeye seasonal distribution estimates by Beauchamp et al. (1999) of 15–18 m and Eggers (1978) of 20–40 m. In the winter months, sockeye tend to aggregate in the shallower littoral zones of the lake; however, during this time of year Lake Washington is isothermal and there is little difference between surface temperatures and temperatures at 20 m. Thus, the annual temperatures at 20 m are reasonably representative of temperatures experi-

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Table 2. Inputs to the bioenergetics and mass balance models.

	Fatty acids[a] (±SD)		Bioenergetics parameters	
	EPA content (mg·g wet wt.$^{-1}$)	DHA content (mg·g wet wt.$^{-1}$)	P:C (by weight)	Energy density (J·g wet wt.$^{-1}$)
Daphnia	0.70 (±0.04)	0.02 (±0.03)	0.018[b]	2281[c]
Daphnia with eggs	0.84 (±0.31)	0.21 (±0.31)	—	2281[c]
Epischura	1.04 (±0.24)	1.40 (±0.27)	0.023[d]	3004[c]
Cyclops	0.60 (±0.70)	3.05 (±2.87)	0.013[e]	3028[c]
Diaptomus	1.08 (±0.97)	0.63 (±0.48)	0.007[e]	3075[c]
Oncorhynchus nerka (liver)	3.67 (±1.76)	5.45 (±2.20)	—	$= 5.234 + 7.75W^{f}$
Oncorhynchus nerka (dorsal)	1.22 (±0.21)	3.20 (±0.83)	0.024[g]	$= 5.234 + 7.75W^{f}$

Note: Values of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) are reported as wet weight and standard deviations (SD). P:C = ratio of phosphorus to carbon; wet wt. = wet weight.

[a]All fatty acid values obtained in present study.
[b]Brett et al. (2000).
[c]Energy densities are averages from representative genera from Cummins and Wuycheck (1971).
[d]Elser et al. (2000).
[e]Hessen and Lyche (1991), Fig. 1.
[f]Equation for sockeye of ≤196 g wet weight, where W represents wet weight (Beauchamp et al. 1989).
[g]Value calculated from 0.3648% P, wet weight (Donaldson 1967), and 14.69% C, wet weight (present study).

Fig. 1. Historical weight data from Woodey (1972) for sockeye (*Oncorhynchus nerka*) in Lake Washington compared with more recent data. The data were fit using a 4th-order polynomial equation.

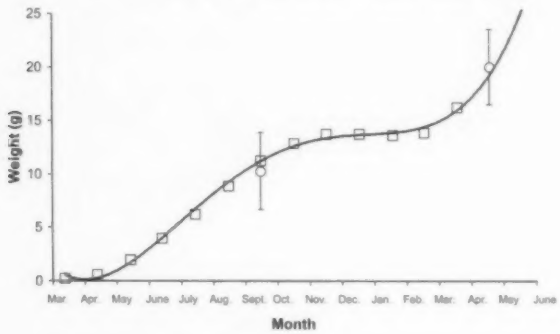
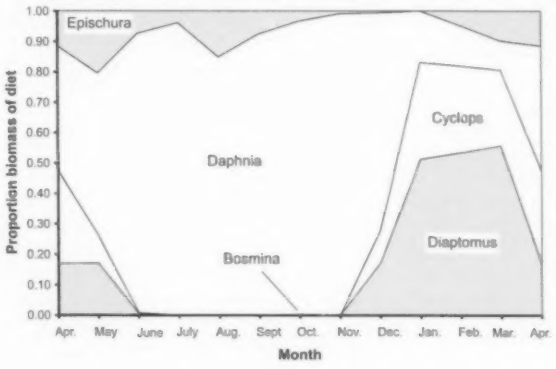


Fig. 2. Composition of sockeye (*Oncorhynchus nerka*) diet in Lake Washington. Based on stomach content data that were transformed into monthly averages and multiplied by the following individual weights (± standard deviation) in µg to obtain percent biomass of each prey genus in the diet: *Epischura*, 36.6 (±10.10); *Daphnia*, 35.3 (±12.80); *Bosmina*, 1.0 (±1.56); *Cyclops*, 4.8 (±.04); *Diaptomus*, 4.7 (±1.33).



enced by sockeye throughout their lacustrine growth. A fourth-order polynomial was fit to the temperature data at 20-m depth to predict daily temperatures for input to the model. Simulations were also run at optimal temperature (15°C), which is the temperature of maximum growth, provided a maximum ration of food (Brett et al. 1969) and optimal lake temperatures (≤15°C) for comparison. Model simulations were run for the 13-month lacustrine growth period from March to the following May, and the potential for growth limitation resulting from dietary availability of the fatty acids EPA and DHA as well as phosphorus was evaluated.

Results

Field sampling

By comparing the biomass estimates of prey taxa in the sockeye diet (Fig. 2) with the Ivlev electivity indices (Fig. 3), it is apparent that although *Epischura* may be selected for, their contribution in terms of biomass to the total diet is comparatively small. Furthermore, the copepods *Cyclops* and *Diaptomus* constitute a large portion of the diet biomass, especially in the winter months, despite their negative electivity indices. More importantly, however, *Daphnia* constitute approximately 90% of the biomass in the diet of Lake Washington sockeye throughout their growing season (June–November).

There was very little variability in the amount of α-linolenic acid (ALA, 18:3 ω3) among all prey types (Fig. 4*a*) and the EPA content of all prey types measured was also very similar (Fig. 4*b*). The highest variability in measurements of EPA was observed in *Diaptomus* and *Cyclops*. The highest total ω3 content was observed in *Cyclops* (Fig. 4*d*). According to the ANOVA, there were no significant differences in EPA, ALA, or total ω3 contents among the different prey types. Zooplankton DHA content was more variable among prey types compared with the other fatty acids measured, with the highest intrageneric variability observed within *Cyclops* (Fig. 4*c*). High variability of DHA concentrations in *Cyclops* was probably the result of a small sample mass

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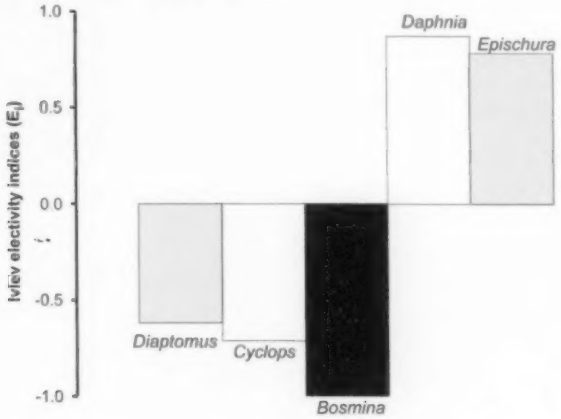
Fig. 3. Ivlev electivity indices calculated for the five dominant genera in Lake Washington sockeye (*Oncorhynchus nerka*) diet. Positive indices suggest that a prey item is selected for relative to its ambient abundance and negative indices suggest that a prey item is selected against. Calculations based on data collected from 1974–1975 (Eggers 1982).



(210–304 μg) analyzed for fatty acids. Significant differences in DHA content among prey groups were substantiated by the ANOVA and the subsequent Tukey test (p = 0.05), which were attributed to the disparate levels of DHA in *Daphnia* and *Cyclops*. *Daphnia* were practically devoid of DHA, whereas the highest observed concentrations of DHA were in *Cyclops*. Because of the shift in prey taxa consumed during the sockeye growth season, pronounced fluctuations in the relative amounts of dietary DHA and P:C ratios are experienced (Fig. 5). The diet of sockeye during winter is dominated by copepods and characterized by low P:C ratios and high DHA, whereas *Daphnia* are more prevalent in the diet during summer months resulting in high P:C ratios and low DHA content. Because there is relatively low variability among prey in EPA content, the content of EPA in the diet remains fairly constant throughout the year.

Sockeye dorsal muscle contained approximately half the amount of fatty acids as the liver tissue (Fig. 6*a*). The content of EPA and DHA were higher in sockeye liver tissue (Fig. 6*b*) than contents found in most of the prey types, except *Cyclops*, which had very high levels of DHA. There was also an increasing trend in all of the fatty acids until a fork length of about 110 mm, after which the fatty acid content declined. This trend was the most pronounced in the liver tissue. Resident kokanee liver and dorsal tissue samples had relatively low essential fatty acid content.

Bioenergetics modeling

Observed growth was consistently below the predicted maximum growth rate for all simulations. However, observed growth did approach maximum potential growth rates in the month of June. Predicted maximum growth greatly exceeded observed growth in the first April of lacustrine development. This could be an artifact of field sampling bias that may have undersampled fish <50 mm in fork length; thus, resulting in an underestimate of newly emergent fry growth rates (Woodey 1972). Growth limitation resulting from dietary EPA was not predicted during any month (Fig. 7*a*). This is evidenced by the fact that observed growth was always less than predicted EPA-limited growth. Moreover, the predicted EPA-limited growth always exceeded maximum growth, suggesting growth limitation resulting from EPA content is highly unlikely.

In contrast, the results for the other essential fatty acid DHA suggest that sockeye in Lake Washington may experience limited growth resulting from the DHA content of their diet much of the year (Fig. 7*b*). Based on these simulations growth appears to be limited by dietary DHA in all months except April, when DHA-limited growth coincides with optimal growth, and in the winter months, when observed growth is negligible. To test this assertion, we conducted a sensitivity analysis of the bioenergetics model by rerunning the simulations using the maximum observed measurements of DHA in *Daphnia* spp. (0.76 mg·g wet wt.$^{-1}$) and maintaining all other variables constant. These simulations were run for the months of greatest reported growth limitation (May–August). The results were consistent with our initial findings and indicate that even if we consider the scenario in which sockeye are feeding on the most nutritious *Daphnia* spp. available (i.e., individuals with the highest DHA content) they are still predicted to experience growth limitation because of insufficient DHA in their diet. Therefore we may conclude that sockeye in Lake Washington are predicted to experience DHA-limited growth, even if we consider the uncertainty of our parameters.

Model predictions of growth based on ratios of P:C in the diet of sockeye were similar to those for EPA and revealed no apparent limitation (Fig. 7*c*). At no point during the year did sockeye growth in Lake Washington appear to be limited by the amount of phosphorus in their diets. Suboptimal temperatures (i.e., temperatures <15°C) experienced by sockeye appeared to have little effect on their growth. Differences in predicted growth for the three temperature scenarios, ambient (at 20 m), optimal lake temperature (≤15°C), and optimal temperature (15°C), were negligible. Therefore, if we partition out the limitation effects of lake temperature, food quantity, and food quality, in terms of DHA content, we can see how much each one of these factors potentially inhibits the growth of sockeye in Lake Washington during different months of the year (Table 3). Based on this comparison, it is evident that food quality, in terms of DHA, is potentially limiting to sockeye growth from May to November and that during the winter months suppressed growth may be due to insufficient food quantity.

Discussion

The results of this study suggest that sockeye growth rates in Lake Washington may be limited by food quality, especially the DHA content, of their diet. This is due to the disproportionate amount of DHA in sockeye compared with their prey. Sockeye are rich in DHA and their diet is composed mostly of *Daphnia*, which are deficient in DHA. Taxa considered to be lacking in phosphorus and of low nutritional value, such as *Cyclops*, had an abundance of EPA and the highest levels of DHA and yet are not heavily preyed upon by sockeye. Conversely, *Daphnia*, which are relatively rich in phosphorus, contained little EPA and were practically devoid of DHA. This is especially true for *Daphnia* without

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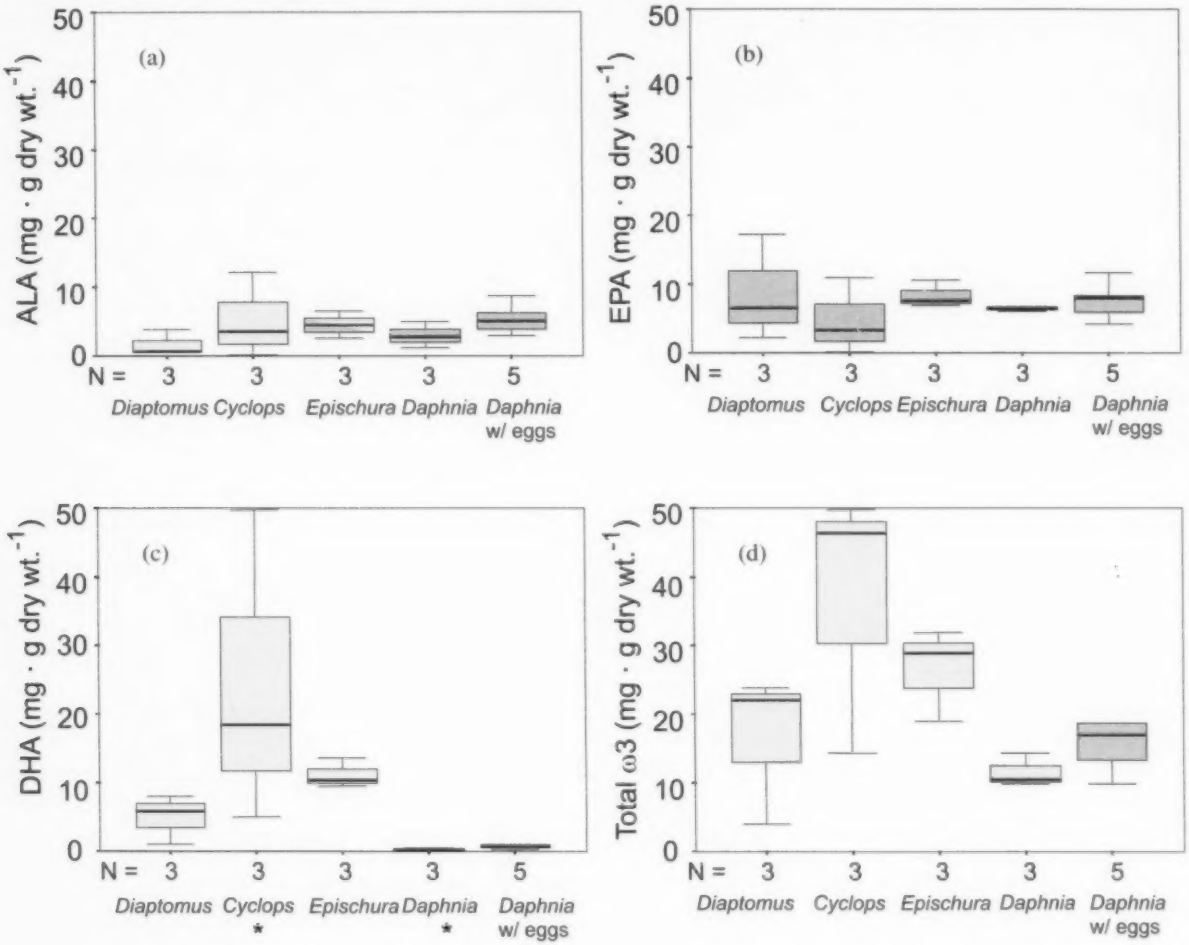
Fig. 4. Box-and-whisker plots of (*a*) 18:3 ω3 (ALA, alpha-linolenic acid), (*b*) EPA (eicosapentaenoic acid), (*c*) DHA (docosahexaenoic acid), and (*d*) total ω3 content of sockeye (*Oncorhynchus nerka*) prey types with sample sizes listed on the *x* axis (w/ eggs = with eggs). The lines through the boxes show the median, the outer edges correspond with the 25th and 75th percentiles, and the whiskers represent the 10th and 90th percentiles. Asterisks (*) identify prey types with significantly different contents of DHA. The sample size (*N*) appears on the *x* axis. Each sample consisted of 50–100 individual zooplankton.



eggs. This disparity in the relative amounts of phosphorus with respect to essential fatty acids in copepods and cladocerans may have implications for the growth of other freshwater planktivorous fish, particularly taxa with high somatic DHA content. Furthermore, fatty acids appear to play a metabolic role in the physiological changes associated with smoltification as accumulations of fatty acids increase markedly up to smolt size (~120 mm), especially in the liver, and then subsequently decline.

Based on the Ivlev electivity indices, sockeye select for the phosphorus-rich *Daphnia* spp., which contain very little DHA, especially those without eggs, and avoid the relatively phosphorus-deficient copepods (*Cyclops* spp. and *Diaptomus*), which have a higher DHA content. One may infer from this result that phosphorus is an important constraint on sockeye growth and they avoid this constraint by selecting the most phosphorus-rich zooplankton available. However, there are many confounding behavioral and physiological factors affecting this predator–prey interaction. For instance, *Daphnia* spp. have a slower swimming response, rendering them much more vulnerable to sockeye predation than copepods, which are more adept at evading predators (Vinyard et al. 1982). In addition, egg-laden *Daphnia* may be more conspicuous to predators and less adept at evading predation; further, *Daphnia* bearing eggs appear to have slightly higher levels of DHA. Thus for behavioral reasons it is logical that sockeye would select for *Daphnia* irrespective of their phosphorus or DHA content. *Daphnia* are also the most abundant prey taxa present in the lake during the spring and summer and their spatial distributions coincide with sockeye; therefore, they are frequently encountered.

In the analysis conducted by Schindler and Eby (1997), one of the few fish species predicted to experience phosphorus-limited growth was sockeye feeding exclusively on cope-

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Fig. 5. Seasonal amounts of P:C (triangles), EPA (eicosapentaenoic acid; squares), and DHA (docosahexaenoic acid; diamonds) in the sockeye (*Oncorhynchus nerka*) diet based on weighted averages of zooplankton from the diet.

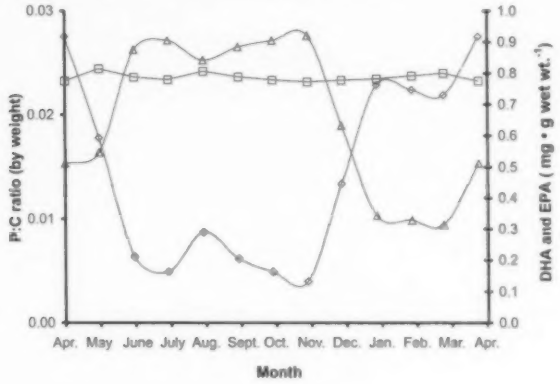
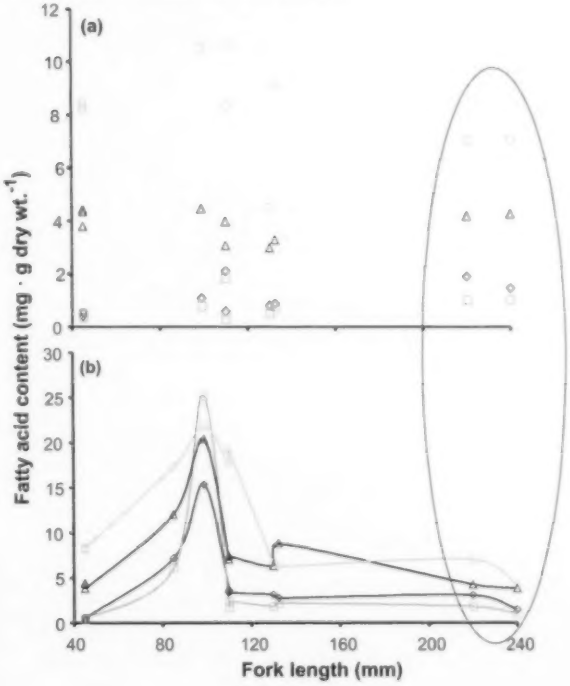
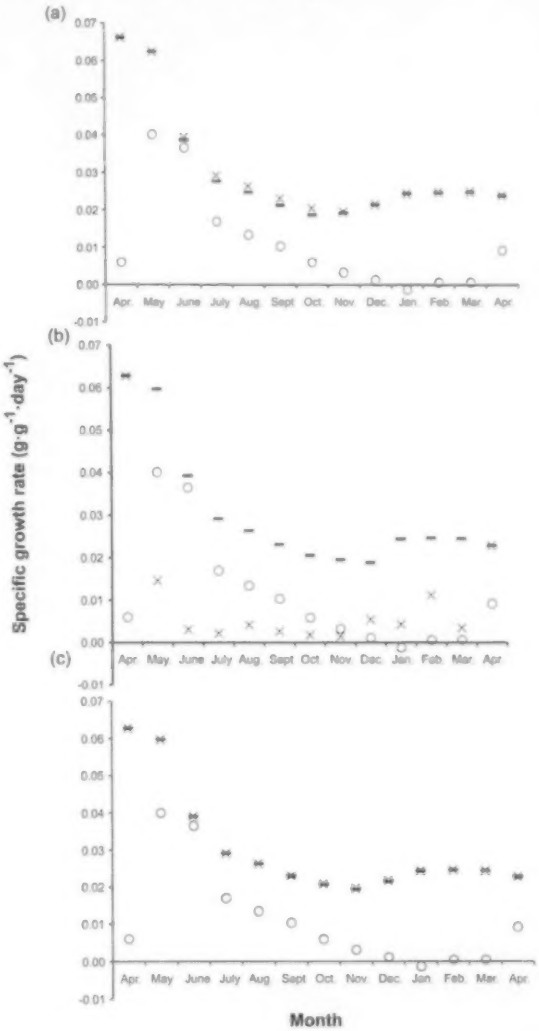


Fig. 6. Content of specific fatty acids in (*a*) the dorsal muscle and (*b*) liver tissue of sockeye salmon (*Oncorhynchus nerka*) from Lake Washington. Specific fatty acids are 18:3 ω3 (diamonds), 18:4 ω3 (squares), EPA (eicosapentaenoic acid; triangles), and DHA (docosahexaenoic acid; circles). Kokanee are the nonanadromous form of sockeye.



pods. According to their analysis, Lake Washington sockeye were not growth limited because their diet was dominated by phosphorus-rich *Daphnia* spp. Their results are corroborated by those of the present analysis, which was conducted at a greater resolution (i.e., monthly intervals), with much more descriptive diet data and using prey ratios of P:C. Although the diet of sockeye in Lake Washington consists primarily of the phosphorus-poor *Diaptomus* for 5 months during their lacustrine development, this is during winter months when growth is suppressed by low prey abundance and phosphorus demands are low.

Fig. 7. Specific growth rate scenarios plotted for actual observed growth, maximum growth at optimal consumption, and (*a*) EPA (eicosapentaenoic acid) limitation, (*b*) DHA (docosahexaenoic acid) limitation, and (*c*) phosphorus limitation (P:C); respective limitation indicated with an × on each panel; open circles = observed; dashes = maximum. All simulations were conducted for the 13-month period of lacustrine development of sockeye salmon (*Oncorhynchus nerka*) in Lake Washington.



The assimilation efficiency of polyunsaturated fatty acids in salmon is quite high (0.93) relative to the assimilation efficiency of other elements, such as nitrogen (0.80; Brett and Groves 1979) and phosphorus (0.74; Nakashima and Legget 1980). This marked difference could be interpreted as a

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Table 3. Percentage of limitation resulting from lake temperature, food quantity, and food quality (docosahexaenoic acid, DHA) to growth of sockeye in Lake Washington.

	Temperature, %	Quantity, %	DHA, %
April	6	94	0
May	12	0	88
June	0	26	74
July	0	0	100
August	0	0	100
September	0	0	100
October	0	0	100
November	0	0	100
December	13	21	66
January	0	21	79
February	0	44	56
March	2	11	87
April	7	93	0

greater evolved affinity for polyunsaturated fatty acids in the diet compared with nitrogen or phosphorus or that polyunsaturated fatty acid molecules are more easily metabolized. However, as polyunsaturated fatty acids are utilized to form cell membranes, as precursors for important metabolites, and as an energy source, this high assimilation efficiency is not surprising. Moreover, as many polyunsaturated fatty acids are unable to be synthesized endogenously, their high assimilation efficiency would be expected.

The growth curve of sockeye is quite unusual. Unlike most vertebrates that experience their greatest exponential growth immediately after birth, sockeye experience their highest growth rates after smoltification upon reaching the ocean (Weatherley and Gill 1995). The a priori explanation of this is that there is a greater abundance of food in the marine environment. However, if we compare the content of EPA and DHA in the freshwater prey of sockeye with that of their marine prey (Table 4), a clear disparity emerges. As evidenced here, freshwater prey species have substantially less highly unsaturated fatty acids than their marine counterparts, especially the freshwater insects, which have less EPA and virtually no DHA. In contrast, marine species, such as euphausids, mysids, and molluscs, are extremely rich in EPA and DHA. This disparity between the essential fatty acid content of marine and freshwater prey may explain the observation that freshwater fish are more adept at elongating precursors to form EPA and DHA than are marine fish (Watanabe 1982).

It is also thought that sockeye have a lower food conversion efficiency in fresh water (20.6%) compared with the food conversion efficiency (27.0%) during their marine growth (Brett 1995). When sockeye are growing at their greatest specific growth rate in Lake Washington, they are feeding almost exclusively on *Daphnia*; however, the essential fatty acid content of *Daphnia* is relatively low compared with other freshwater prey and very low compared with marine prey taxa. These two lines of evidence, in conjunction with the bioenergetics modeling results, suggest an alternative hypothesis to limited growth of sockeye in the freshwater environment, perhaps the allocation of carbon to growth is governed by how much carbon is available in the form of essential fatty acids.

According to the model simulations presented, sockeye are DHA limited to such an extent that they must be provided with an alternative source of DHA to grow at the observed growth rates. Sockeye can avoid DHA limitation by either complimenting their diet with other zooplankton species that are richer in DHA or through the elongation of the shorter length fatty acids linolenic (18:3 ω3) acid and EPA (20:5 ω3). The former scenario is not likely in Lake Washington as sockeye are feeding almost exclusively on *Daphnia* in the spring and early summer. It is generally believed that freshwater fish species are more adept at elongating shorter chain essential fatty acids than marine fish species, which may lack the necessary enzymes and desaturases for elongation (Watanabe 1982). This is true of the marine species *Scophthalamus maximus* (turbot; Ghioni et al. 1999), which is much less efficient at elongating ω3 fatty acids than Atlantic salmon (*Salmo salar*), although both of these species were limited in their ability to biosynthesize DHA from shorter carbon chain precursors. The conversion of EPA and linolenic acid to longer chain DHA in rainbow trout (*O. mykiss*) has been definitively confirmed by using radiotracer (^{14}C) studies (Buzzi et al. 1996). It is quite possible that luxury uptake and subsequent elongation of EPA, which was not found to be limiting to sockeye growth, may account for the DHA required to sustain observed growth rates. However, trout fed on diets rich in ω3 fatty acids had 20 times more DHA in their hepatocytes at the conclusion of the experiment, implying that trout had much more DHA that could be metabolized when it was supplied in their diet than when dependent on elongation. The inefficiency in the conversion of shorter essential fatty acids has been verified in Atlantic salmon, in which it is thought that the rates of elongation may be insufficient to meet the metabolic needs of growth. Moreover, Atlantic salmon raised on diets deficient in essential fatty acids often suffer from pale swollen livers and fin erosion (Ruyter et al. 2000*b*). Although elongation is known to occur in salmonids, there appear to be metabolic costs associated with the elongation of existing fatty acids, and higher growth rates in salmonids are still observed when these HUFA are supplied directly in the diet (Takeguchi and Watanabe 1982; Ruyter et al. 2000*b*). Further efforts should be made to quantify the elongation efficiency of these essential fatty acids with respect to salmonids.

The gradual increase in essential fatty acids in the liver of sockeye throughout their development leading up to smoltification and the subsequent decline is indicative of the physiological demands associated with smoltification. The relatively low concentrations of essential fatty acids among kokanee may be indicative of fat stores being utilized by fish overwintering in the lake. Among the essential fatty acids, stearidonic acid (18:4 ω3) was observed to fluctuate the most. As this fatty acid is one of the precursors for elongation to form EPA and DHA, as well as an intermediate in the oxidation of HUFA to lesser fatty acids yielding energy, it is not surprising that this particular fatty acid fluctuates most with sockeye size.

The catabolism of lipids yields 9 $kcal \cdot g^{-1}$ compared with carbohydrates and proteins, which yield only 6 $kcal \cdot g^{-1}$, thus lipids constitute the most efficient means of storing energy (Stryer 1981). For this reason lipids provide the energy for

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Table 4. Eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) contents (% total fatty acids) of various freshwater and marine prey taxa of salmonids (revised from Higgs et al. 1995 and references therein).

Freshwater prey taxa	EPA	DHA	Marine prey taxa	EPA	DHA
Insecta			**Crustacea**		
Diptera	7.7	0.0	*Calanus helgolandicus*	14.3	15.4
Trichoptera	6.5	0.0	*Palandus jordani*	18.0	10.1
Coleoptera	4.3	0.0	*Eugommarus confervicolus*	14.5	6.8
Ephemeroptera	12.5	0.0	*Corophium volutator*	25.8	7.1
Plecoptera	13.9	0.0	*Euphausia pacifica*	20.5	12.3
Hymenoptera	0.0	0.0	*E. pacifica* (California)	30.9	6.4
Odonata	9.4	0.0	*E. pacifica* (Washington)	27.9	16.1
Crustacea			*E. gibboides*	10.3	21.0
Cladocera	9.2	1.5	*E. brevis*	14.9	24.4
Daphnia cucullata	11.1	1.4	*E. americana*	13.5	19.5
Daphnia magna	13.9	0.0	*E. krohnii*	14.0	21.9
Daphnia spp.†	13.7	1.5	*E. superba*	25.3	14.6
Cyclops strenuus	8.8	16.8	*Thysanoessa inermis*	21.4	10.9
Cyclops spp.†	5.4	20.0	*Neomysis integer*	20.9	11.0
Epischura nevadensis†	14.9	20.2	*N. integer* (with eggs)	26.9	12.6
Eudiaptomous gracilis	8.8	8.8	*N. spinosa*	24.0	9.0
Mean	9.3	4.7	*N. awatschensis*	17.4	11.3
Standard deviation	4.2	7.8	*N. nakazawai*	21.1	10.5
			Mollusca		
			Loligo opalensis	12.8	29.6
			Squid (whole)	17.7	31.1
			Mean	19.6	15.1
			Standard deviation	5.8	7.3

Note: Taxa denoted by † are values from this study.

many metabolic functions and should be considered one of the major currencies of bioenergetics. The total lipid contained in the liver of some fishes has been used to accurately predict their recruitment (Marshall et al. 2000). More extensive research should focus on the importance of lipids in the physiological ontogeny of fish species with an emphasis on essential fatty acids.

Based on the results of this study, we can prioritize the factors most likely limiting sockeye growth. We may conclude that food quality, especially the DHA content of the diet, may limit sockeye growth for a good portion of their lacustrine development, depending on their ability to elongate shorter chain length unsaturated fatty acids. Furthermore, a high P:C ratio in the diet of sockeye makes it improbable that growth is ever limited by phosphorus. The second most important factor in the limitation of sockeye growth in Lake Washington is food availability. During the winter months, sockeye may be growing at suboptimal rates because they are not feeding near maximum consumption (i.e., low food abundance). Finally, we may conclude that even though sockeye aggregate at depths where they experience less than ideal temperatures for growth, these temperatures do not substantially limit their growth. Thus, the avoidance of piscivorous predators such as northern pikeminnow (*Ptychocheilus oregonensis*) and cutthroat trout (*Oncorhynchus clarki*) in addition to prey distribution are probably more important in controlling the vertical distribution of sockeye in Lake Washington than is temperature.

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Chemosterilization of male sea lampreys (*Petromyzon marinus*) does not affect sex pheromone release

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Abstract: Release of males sterilized by injection with bisazir is an important experimental technique in management of sea lamprey (*Petromyzon marinus*), an invasive, nuisance species in the Laurentian Great Lakes. Sea lampreys are semelparous and sterilization can theoretically eliminate a male's reproductive capacity and, if the ability to obtain mates is not affected, waste the sex products of females spawning with him. It has been demonstrated that spermiating males release a sex pheromone that attracts ovulating females. We demonstrated that sterilized, spermiating males also released the pheromone and attracted ovulating females. In a two-choice maze, ovulating females increased searching behavior and spent more time in the side of the maze containing chemical stimuli from sterilized, spermiating males. This attraction response was also observed in spawning stream experiments. Also, electro-olfactograms showed that female olfactory organs were equally sensitive to chemical stimuli from sterilized and nonsterilized, spermiating males. Finally, fast atom bombardment mass spectrometry showed that extracts from water conditioned with sterilized and nonsterilized, spermiating males contained the same pheromonal molecule at similar levels. We concluded that injection of bisazir did not affect the efficacy of sex pheromone in sterilized males.

Résumé : La libération de mâles stérilisés à l'aide d'injections de bisazir est une technique expérimentale importante dans la gestion de la grande lamproie marine (*Petromyzon marinus*), une espèce envahissante et nuisible dans les Grands-Lacs laurentiens. Les lamproies sont sémelpares et la stérilisation peut en théorie éliminer la capacité reproductive du mâle et, si la possibilité d'obtenir des mâles n'est pas affectée, elle peut gaspiller les produits sexuels de la femelle qui fraye avec lui. Il a été démontré que les mâles pendant la spermiation libèrent une phéromone sexuelle qui attire les femelles en ovulation. Nous montrons que des mâles stérilisés émettent aussi la phéromone durant la spermiation et qu'ils attirent des femelles en ovulation. Dans des labyrinthes à deux choix, les femelles en ovulation accroissent leur comportement de recherche et passent plus de temps du côté du labyrinthe qui contient les stimulus chimiques provenant des mâles stérilisés en spermiation. Cette réaction d'attraction s'observe aussi dans des expériences dans le cours d'eau de fraye. De plus, des électro-olfactogrammes indiquent que les organes olfactifs de la femelle sont également sensibles aux stimulus chimiques de mâles en spermiation, qu'ils soient stérilisés ou non. Enfin, la spectrométrie de masse à bombardement atomique rapide révèle que des extraits d'eau conditionnés avec des mâles en spermiation, tant stérilisés que non stérilisés, contiennent la même molécule de phéromone à des concentrations semblables. En conclusion, l'injection de bisazir n'affecte pas l'efficacité de la phéromone sexuelle chez les mâles stérilisés.

[Traduit par la Rédaction]

Introduction

The sea lamprey (*Petromyzon marinus*) is a nonindigenous, nuisance species in the Laurentian Great Lakes and a potentially lethal parasite feeding on the blood of larger fishes such as lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*). Its establishment in the upper Great Lakes during the 1920s through 1940s was a significant factor in the collapse of commercial fisheries and brought about dramatic biological and ecological changes in the fish communities (e.g., Smith 1971; Coble et al. 1990). Despite an intensive program started in the 1950s to control their populations (Smith and Tibbles 1980), the sea lamprey remains a factor in the mortality of larger fishes in the Great Lakes (e.g., Spangler et al. 1980; Kitchell 1990).

An important new method being experimentally implemented in sea lamprey management is the sterile male release technique (e.g., Bergstedt et al. 2003; Schleen et al. 2003;

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Twohey et al. 2003*a*). In this technique, the chemosterilant bisazir (*P*,*P*-bis(1-azirindinyl)-*N*-methylphosphinothioic amide) is injected intraperitoneally into adult males (Hanson and Manion 1978). Sperm from males injected with bisazir can still fertilize eggs, but the resulting embryos die before reaching the larval stage (Hanson and Manion 1980). Laboratory and field studies with bisazir treatment demonstrated that sterilized males mate successfully with females (Hanson and Manion 1978) and when released into spawning streams reduce the abundance of sea lamprey offspring (Bergstedt et al. 2003). In the current application of the sterile male release technique, the observed proportion of sterilized males in male spawning populations was typically near expected values calculated by mark and recapture estimates, but the overall percent egg viability was consistently higher than the theoretical effect of the number of sterilized males released (Bergstedt et al. 2003). One factor potentially contributing to the difference between the actual and theoretical egg viability could be the effect of bisazir on pheromone production of male sea lampreys. Nonsterilized, spermiating male sea lamprey release the potent sex pheromone 7α,12α,24-trihydroxy-5α-cholan-3-one 24-sulfate, which induces preference and locomotor activities of ovulating females (Li et al. 2002). This pheromone functions to attract females that are ready to spawn. Clearly, if bisazir affected the release of this pheromone, the ability of sterilized males to attract mates would be reduced. The present study explores this possibility.

As invasive fish species increasingly threaten the health of our aquatic ecosystems, the sterile male release technique is one of the few potential control methods with no identifiable environmental effects. It has the potential to become an important technique in management of these nuisance species, for which bisazir could be used as a sterilant. Where studied, most fish species are shown to rely heavily on the olfactory sense to mediate reproduction (e.g., Solomon 1977; Liley 1982; Stacey et al. 1994). Although each species would have to be tested independently, initial determination of whether sterilization of sea lampreys with bisazir affects sex pheromone biosynthesis and release would bear strongly on its potential for broader use.

The overall goal of this study was to determine if bisazir-sterilized, spermiating male sea lampreys release the same sex pheromone at similar levels found in nonsterilized, spermiating males and if they elicit the same behavioral response from adult sea lampreys. We applied a multidisciplinary approach to characterize whole animal and electrophysiological responses to, as well as chemistry of, chemical stimuli produced by sterilized males. The following specific questions were posed. (*i*) In a two-choice maze, do ovulating females show preference and searching behaviors when exposed to water conditioned with bisazir-sterilized, spermiating males? (*ii*) In a spawning stream, are female sea lampreys attracted to water conditioned with bisazir-sterilized, spermiating males? (*iii*) Do female olfactory organs show the same electrophysiological response to water conditioned with bisazir-sterilized and nonsterilized, spermiating males? (*iv*) Do extracts of water conditioned with bisazir-sterilized and nonsterilized, spermiating males contain the same pheromone molecule? Our results showed that bisazir-sterilized, spermiating male sea lampreys released the same sex pheromone at similar levels found in nonsterilized, spermiating males.

Materials and methods

Collection and maintenance of animals

Adult sea lampreys were collected from tributaries to Lakes Huron and Michigan by the staff of the U.S. Fish and Wildlife Service, Marquette Biological Station, Marquette, Mich. The animals were transported to the sterilization facility and main laboratory at the U.S. Geological Survey, Hammond Bay Biological Station, Millersburg, Mich. Males were identified by their raised dorsal ridge, and females by their enlarged, soft abdomen and absence of dorsal ridge (Vladykov 1949). Males averaged 470 mm and 233 g, whereas females averaged 465 mm and 240 g. The sexes were separated and held in flow-through tanks (1000 L) with Lake Huron water (7°C to 20°C).

Sterilization of male sea lampreys

Males were sterilized in the sterilization facility by robotic injection with a dose of 100 mg·kg body weight^{-1} of bisazir (Hanson and Manion 1978, 1980; Twohey et al. 2003*a*). Quality assurance monitoring showed that males used during this study received no less than the correct dose of bisazir (Twohey et al. 2003*a*). Sterilized males were held in the sterilization facility for at least 48 h after injection before being used in any procedure.

Identification of maturity

Each sex was further assigned one of two maturity classifications. For males, gentle pressure was applied to the abdomen to induce emissions into a petri dish. White emissions indicated spermiation. Depending on treatment status, males that did not emit sperm were classified as nonsterilized, prespermiating males or as sterilized, prespermiating males. Those that did emit sperm were classified as nonsterilized, spermiating males or as sterilized, spermiating males. To determine whether white emissions correctly indicated spermiation, emissions from 10 males classified as spermiating and 10 classified as nonspermiating were checked under a microscope for sperm. All 20 males were classified correctly. For females, gentle pressure was applied to the abdomen to induce egg emission. Females that did not release eggs were classified as preovulating females and those that did release eggs were classified as ovulating females.

Induction of spermiation and ovulation

Sterilized and nonsterilized males were allowed to spermiate naturally or were induced to spermiate by holding them at 18°C and then injecting them intraperitoneally with [D-Ala^6]-luteinizing hormone-releasing hormone (*p*Glu-His-Trp-Ser-Tyr-D-Ala-Leu-Arg-Pro-Gly-NH_2, Sigma Chemical Co., St. Louis, Mo.) at a dose of 100 μg·kg body weight^{-1} (Li 1994). This injection was repeated 3 and 5 days later. Males were checked each day until spermiation occurred. Females were treated similarly to induce ovulation.

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Chemical stimuli used in experiments

Either male sea lampreys or water conditioned with male sea lampreys were used as the chemical stimuli in experiments. Conditioned water was collected by holding individual males of classification for 4 h in polyethylene buckets filled with 10 L of water. These buckets were aerated and kept in a water bath of 18°C. The conditioned water was either (*i*) used immediately for behavioral assays, (*ii*) frozen immediately at –80°C for subsequent electro-olfactographic analyses, or (*iii*) extracted using C-18 solid-phase extraction cartridges and the elute frozen at –80°C for chemical analysis.

Experiment 1. In a two-choice maze, do ovulating females show preference and searching behaviors when exposed to water conditioned with bisazir-sterilized, spermiating males?

Preference and searching tests were used to assess the attraction behaviors of adult sea lampreys of each sex and maturity class to chemical stimuli produced by sterilized males of both maturity classes. Preference behaviors were measured as the amount of time spent in each side of the maze, and searching behaviors were measured as the amount of time spent swimming at the head of each side of the maze and were categorized as described by Li et al. (2002). These tests were carried out in the same two-choice maze, under similar conditions and following the same protocol of Li et al. (2002). Briefly, in each test, the behavior of a single test subject was videotaped before and after the introduction of chemical stimuli from either sterilized spermiating or prespermiating males into the odor chamber of the side of the maze chosen randomly by coin toss. The chemical stimuli were either five sterilized males per test (placed directly into the odor chamber) or water conditioned with sterilized, spermiating males (delivered into the odor chamber at 75 mL·min^{-1} using a peristaltic pump). Tests were conducted between 0700 and 1700 in water temperatures that ranged from 12 to 24°C.

The times spent in each side of the maze and the time spent swimming at the head of each arm of the maze by the test animal in the treatment (stimulus) and control (no stimulus) side before and after chemical stimulus introduction were summed from the videotapes by a reviewer unaware of which side contained the stimulus. The data were used to calculate an index of preference or searching (*I*), described by Li et al. (2002) for each individual test subject: $I = (A_t/(A_t + B_t)) - (A_c/(A_c + B_c))$, where B_t and A_t are the time spent or time spent searching in the treatment side of the maze before and after chemical stimulus introduction, respectively, and B_c and A_c are the time spent or time spent searching in the control side of the maze before and after chemical stimulus introduction, respectively. These indices compare test subject behavior in each side of the maze before and after chemical stimulus introduction. A positive *I* value indicates a preference or increase in preference or searching behavior, whereas a negative value indicates an avoidance or decrease in the behaviors.

The *I* values were analyzed with a two-tailed Wilcoxon signed rank test (Rao 1998) to determine if there was differences in preference and searching behavior in each combination of test subject and chemical stimulus source class. Sample sizes varied owing to availability of test subjects (Tables 1 and 2). Tests in which proportions and *I* values could not be generated were not used in analyses. These situations composed approximately 20% of all tests and occurred when test subjects did not explore both sides of the maze in the initial recording period or did not explore either side of the maze in the experimental recording period, causing zero index values dictated by the Wilcoxon signed rank test to be deleted.

Experiment 2. In a spawning stream, are female sea lampreys attracted to water conditioned with bisazir-sterilized, spermiating males?

To assess whether sterilized, spermiating male chemical stimuli attract females in their spawning habitat, we monitored ovulating and preovulating female responses to sterilized male chemical stimuli under similar conditions and in the same 65-m section of the Ocqueoc River used by Li et al. (2002). Tests were conducted between 0700 and 1700 in water temperatures ranging from 12 to 24°C using the protocol of Li et al. (2002). A day before testing, a female sea lamprey (ovulating or preovulating) was fitted externally with a radio tag (Model 393, Advanced Telemetry Systems, Isanti, Minn.) according to Kelso and Gardner (2000). The tagged female and the five sterilized, spermiating and five sterilized, prespermiating males were transported to the study site on the following morning. The sterilized, spermiating and sterilized, prespermiating males were randomly assigned to two upstream cages. The tagged female was placed in a downstream acclimation cage, exposed to the two chemical stimuli sources for 2 h, and then released.

In each test, the subject's location was observed visually or determined with a directional radio antenna and receiver (Lotek Engineering Inc., Newmarket, Ont.) and recorded on a map grid of the site every 5 min. If test subjects failed to move from the release site within 1 h, they were removed. If test subjects did move from the release site, they were observed until (*i*) they reached one cage or the other and stayed there for 1 h, (*ii*) they swam past the cages, or (*iii*) 4 h elapsed from the start of the test. A contingency table was used to tally the behavior of ovulating ($N = 15$) and preovulating female ($N = 10$) test subjects. Responses were categorized as swimming to the sterilized, spermiating males, swimming to the sterilized, prespermiating males, or not choosing (staying at an intermediate position within the stream section or not leaving the acclimation cage). A Fisher's exact test was used to compare the choice of females (PROC FREQ; SAS Institute Inc., Cary, N.C.).

Experiment 3. Do female olfactory organs show the same electrophysiological response to water conditioned with bisazir-sterilized and nonsterilized, spermiating males?

The olfactory potency of an L-arginine standard and chemical stimuli from sterilized, spermiating males, nonsterilized, spermiating males, and prespermiating males were examined with electro-olfactogram (EOG) recordings of female sea lampreys. EOG recordings measure summated generator potentials of the olfactory neurons (Ottoson 1956; Getchell 1974). The recordings were conducted according to the pro-

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cedures established by Li et al. (1995). Briefly, a female was anaesthetized with metomidate hydrochloride (3 mg·kg body weight^{-1}) (Syndel, Vancouver, B.C.), immobilized with gallamine triethiodide (150 mg·kg body weight^{-1}) (Sigma Chemical Co., St. Louis, Mo.), and placed in a water-filled trough. The head of the female remained above the water and the gills were supplied with aerated Lake Huron water. The olfactory lamellae were then exposed and perfused with water from a source that could deliver either clean water or the same clean water containing chemical stimuli on demand. Differential electrical responses between the skin surface and the sensory epithelia in response to each chemical stimulus were recorded using two Ag/AgCl electrodes (type EH-1S, World Precision Instruments, Sarasota, Fla.) filled with 3 M potassium chloride and bridged with glass capillary tubes filled with 8% gelatin – 0.9% saline. Two experiments were conducted using this setup.

In the first experiment, we determined dose–response relationships (Li et al. 1995) for water conditioned with sterilized, spermiating ($N = 8$), nonsterilized, spermiating ($N = 8$), and nonsterilized, prespermiating ($N = 4$) males as test stimuli. In a given trial, a 10^{-5} M L-arginine standard was pulsed into the olfactory epithelium of a female for 5 s and the EOG response was measured to establish a baseline of electrical activity. Next, blank control water was introduced and the response was measured to confirm the absence of response from the clean water supply used both to perfuse the olfactory organ and to dilute the chemical stimuli for testing. Increasing concentrations of test stimuli starting at 10^6 times dilution were then introduced and the responses were measured. Measuring the response to the L-arginine standard and blank controls again at the end of the dilution series concluded each trial. The epithelium of each female was allowed to recover at least 3 min between stimuli, and each of the test stimuli concentrations were assayed at least twice on a female. Female EOG response magnitudes were measured in mV and expressed as a percentage of the L-arginine standard.

In the second experiment, we used cross-adaptation as described by Li and Sorensen (1997) to determine the olfactory sensitivity of females to water conditioned with sterilized ($N = 5$) and nonsterilized ($N = 5$), spermiating males. In a given trial, baseline olfactory responses of females to blank control water, a L-arginine standard, and the test stimuli (water conditioned with sterilized and nonsterilized, spermiating males) were recorded using EOG. The test stimuli were used at concentrations that elicited equipotent olfactory responses at about 200% of the L-arginine standard. During adaptation, the olfactory epithelium of the female was continually perfused with the adapting stimulus (either sterilized or nonsterilized, spermiating male test stimuli) for 5 min, after which a 5-s pulse of the same stimulus at the same concentration being used for the adaptation was introduced to the nose to establish that the sensory epithelium was completely adapted. Next, a 5-s pulse of the L-arginine standard was introduced to confirm that the olfactory epithelium of the female was still active. A 5-s pulse of the alternate test stimulus (not being used as the adapting stimulus) was then introduced to see if any responses were generated. Switching the epithelial adapting stimulus back to clean water completed the trial. The epithelium of the female was allowed to recover for 30 min and then it was tested again using the alternate test stimulus as the adapting stimulus. The effects of adaptation on female responses to male stimuli were analyzed with a two-way analysis of variance (ANOVA). Once the main effect of adaptation had been established, effects of each adapting stimulus on olfactory responsiveness to other stimuli were determined by Student's t tests with equal variance (PROC GLM, SAS Institute Inc., Cary, N.C.).

Experiment 4. Do extracts of water conditioned with bisazir-sterilized and nonsterilized, spermiating males contain the same pheromone molecule?

Water conditioned with sterilized ($N = 3$) and nonsterilized ($N = 3$), spermiating males were separately prefiltered with No. 3 Whatman filter paper, passed through methanol-activated C-18 solid-phase extraction cartridges (Waters, Milford, Mass.) and eluted with 100% methanol. All six extracts were assayed for relative abundances of molecules by subjecting them to fast atom bombardment mass spectrometry (10 kV) analyses at both negative and positive ionization modes.

Results

The total time spent and time spent searching by test subjects in the two sides of the maze before chemical stimulus introduction did not differ significantly ($P > 0.10$; data not shown), indicating that adults were not biased to either side. Ovulating females, however, showed strong preference responses to sterilized, spermiating male chemical stimuli (Table 1). Eleven out of 12 ovulating females spent more time in the side of the maze containing five sterilized, spermiating males ($P < 0.01$, $N = 12$), and 9 of 10 ovulating females spent more time in the side containing water conditioned with sterilized, spermiating males ($P < 0.02$, $N = 10$). In contrast, none of the three other classes of test subjects showed a preference response to sterilized, spermiating male chemical stimuli ($P > 0.10$, see Table 1 for sample sizes), and ovulating females did not show a preference response to sterilized, prespermiating male chemical stimuli ($P > 0.10$, $N = 10$; data not shown).

Consistent with the preference results, there was an increase in searching behavior by ovulating females exposed to chemical stimuli from sterilized, spermiating males (Table 2): all eight ovulating females spent significantly more time searching in the side of the maze containing five sterilized, spermiating males ($P < 0.01$, $N = 8$), and seven of eight ovulating females spent significantly more time searching in the side containing water conditioned with sterilized, spermiating males ($P < 0.01$, $N = 8$). In contrast, none of the three other classes of test subjects showed significant increases or decreases in searching behavior ($P > 0.10$, see Table 2 for sample sizes), and ovulating females did not show significant increases or decreases in searching behavior ($P > 0.10$, $N = 8$; data not shown) in response to sterilized, prespermiating male chemical stimuli.

The chemical stimuli released by sterilized, spermiating males influenced the behavior of ovulating females, but not of preovulating females, within the spawning stream section.

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Table 1. Chemical stimuli from sterilized, spermiating male sea lampreys (*Petromyzon marinus*) induced preference responses from ovulating females only.

Test subject	*N*	Preference	*P*	Preference ratio
Ovulating female	12	11	<0.01	7.0 (5.5)
Ovulating female*	10	9	<0.02	2.0 (1.0)
Preovulating female	10	6	NS	1.7 (1.0)
Nonsterilized, spermiating male	11	7	NS	1.4 (1.8)
Nonsterilized, prespermiating male	10	6	NS	2.2 (1.6)

Note: *N*, sample size. Preference is the number of test subjects that spent proportionately more time after stimulus introduction in treatment (scented) side. *P* values were determined using a Wilcoxon signed rank test (two-tailed) using indices of preference. NS, not significant ($P > 0.10$). Preference ratio is the mean ratio (standard deviation) of the time spent in seconds in the treatment or control sides after stimulus introduction. Asterisk (*) indicates ovulating female tests using water conditioned with sterilized, spermiating males as the stimulus source.

Table 2. Chemical stimuli from sterilized, spermiating male sea lampreys (*Petromyzon marinus*) increased searching responses from ovulating females only.

Test subject	*N*	Searching	*P*	Searching ratio
Ovulating female	8	8	<0.01	3.9 (1.5)
Ovulating female*	8	7	<0.01	3.3 (4.0)
Preovulating female	7	3	NS	1.3 (1.3)
Nonsterilized, spermiating male	10	5	NS	0.8 (1.2)
Nonsterilized, prespermiating male	8	5	NS	2.4 (2.7)

Note: *N*, sample size. Searching is the number of test subjects that spent proportionately more time swimming after stimulus introduction in treatment (scented) side. *P* values were determined using a Wilcoxon signed rank test (two-tailed) using indices of preference. NS, not significant ($P > 0.10$). Searching ratio is the mean ratio (standard deviation) of the time in seconds spent swimming in the treatment or control sides after stimulus introduction. Asterisk (*) indicates ovulating female tests using water conditioned with sterilized, spermiating males as the stimulus source.

Females were not biased toward either side of the stream. Among the 15 ovulating females tested, 10 swam to and then stayed at the cage containing sterilized, spermiating males and five did not choose a stimulus source. Of the 10 that did choose, the mean time to swim the 65 m to the sterilized, spermiating males was 29 min. No ovulating females swam to the cage containing sterilized, prespermiating males. Among the 10 preovulating females tested, three swam to the cage containing sterilized, spermiating males, two swam to the cage containing sterilized, prespermiating males, and five did not choose a stimulus source. The distributions of choices differed significantly between ovulating and preovulating females ($P = 0.024$). Although the behavior was not quantified, we observed ovulating females swimming repetitively around and against the cage containing sterilized, spermiating males for 1 h. The three preovulating females that swam to the sterilized, spermiating male cage and the two that swam to the sterilized, prespermiating male cage did not display this behavior but paused briefly at the cages and continued swimming upstream.

In EOG experiments, the chemical stimuli released by sterilized ($N = 8$) and nonsterilized ($N = 8$), spermiating males induced similar responses from the olfactory epithelium of adult females, but chemical stimuli from nonsterilized, prespermiating males ($N = 4$) did not at equivalent concentrations (Fig. 1). Both sterilized and nonsterilized, spermiating male conditioned waters had detection thresholds of approximately 10^5 times dilution. The detection threshold for nonsterilized, prespermiating male chemical stimuli was approximately 10^2 times dilution, one thousand times more concentrated than the dilution required for detection of sterilized and nonsterilized, spermiating male chemical stimuli.

Cross-adaptation experiments demonstrated that female olfactory responses were affected by continuous exposure to spermiating male chemical stimuli (ANOVA; $P < 0.01$). Although the responses to L-arginine standard did not significantly change before and during adaptation (Student's *t* test; $P > 0.05$), there were substantial differences among responses to sterilized and nonsterilized, spermiating male chemical stimuli before and during adaptation (Student's *t* test; $P < 0.01$). Both sterilized and nonsterilized, spermiating male chemical stimuli suppressed olfactory responsiveness to themselves and each other when used as adapting stimuli (Fig. 2*a*). For example, when sterilized spermiating male chemical stimuli (Fig. 2*b*; $N = 5$) were used as the adapting stimuli, the initial responses were 2.17 ± 0.23 mV for sterilized, spermiating male chemical stimuli and 1.52 ± 0.39 mV for nonsterilized, spermiating male chemical stimuli, whereas during adaptation, the responses of sterilized, spermiating male chemical stimuli to itself was 0.08 ± 0.02 mV and to nonsterilized, spermiating male chemical stimuli was 0.18 ± 0.13 mV. When nonsterilized, spermiating male chemical stimuli were used as the adapting stimulus (Fig. 2*c*; $N = 5$), the same pattern of olfactory suppression occurred for each chemical stimulus.

Negative and positive fast atom bombardment mass spectrometry showed that the base peak (the most abundant molecule) of crude extracts of all three samples of water conditioned with sterilized, spermiating males had a molecular mass of 472 Da, the same as extracts from the three sam-

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Fig. 1. (*a*) Representative electro-olfactogram (EOG) responses of female sea lampreys (*Petromyzon marinus*) to chemical stimuli from sterilized, spermiating males (SSM, solid diamonds), nonsterilized, spermiating males (SM, open circles), and nonsterilized, prespermiating males (PSM, solid circles). Std, the response to a 10^{-5} M L-arginine (L-arg) standard; Con, the response to a blank water control. Numbers along the *x* axis indicate the logarithmic value of the dilution from the original conditioned water collected by holding one male in 10 L for 4 h. (*b*) Female sea lamprey EOG dose–response relationships to SSM ($N = 8$), SM ($N = 8$), and PSM ($N = 4$) chemical stimuli. Responses are measured as a percentage of the response to a 10^{-5} M L-arginine standard. Vertical bars represent one standard error.

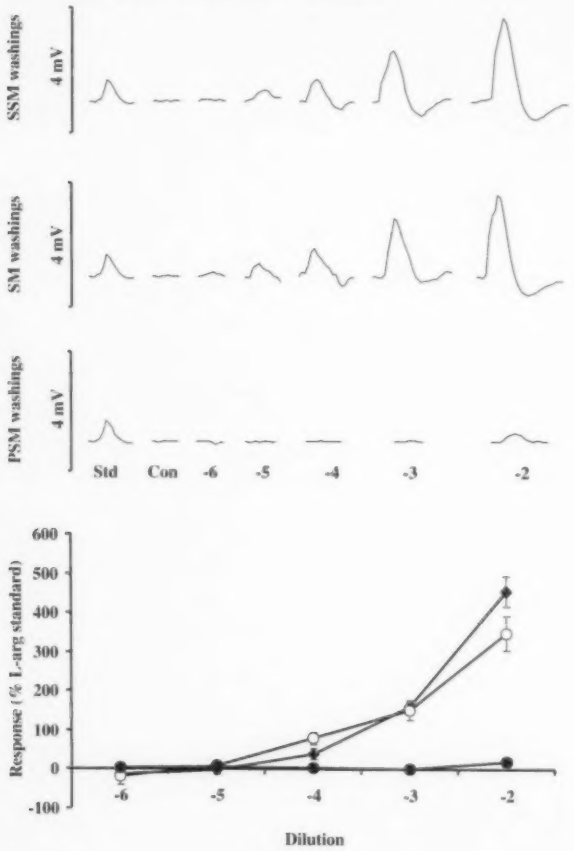
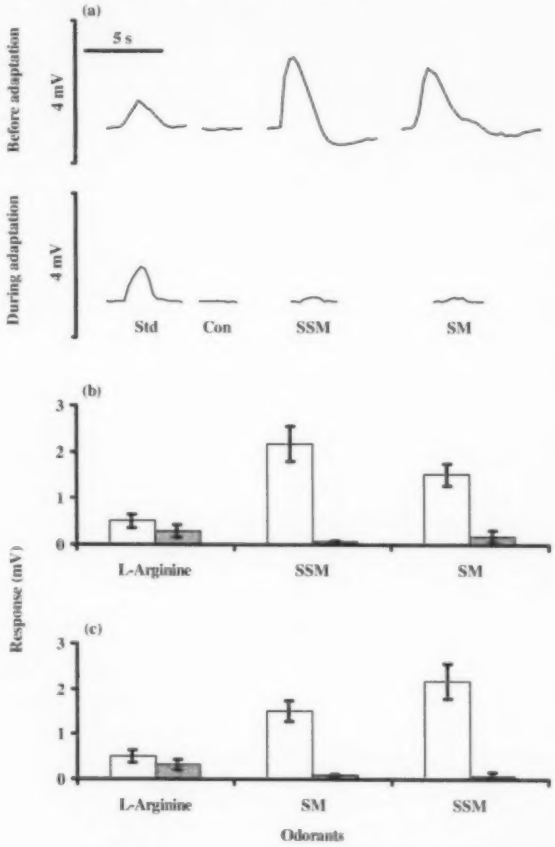


Fig. 2. (*a*) Representative electro-olfactogram (EOG) responses of female sea lampreys (*Petromyzon marinus*) to chemical stimuli from sterilized, spermiating male (SSM) and nonsterilized, spermiating male (SM) before (open bars) and during (shaded bars) adaptation to a SSM chemical stimuli. Std, the response to a 10^{-5} M L-arginine standard; Con, the response to a blank water control. Female EOG responses to a 10^{-5} M L-arginine standard, SSM and SM chemical stimuli both before and during adaptation to (*b*) SSM and (*c*) SSM chemical stimuli were measured. Vertical bars represent one standard deviation.



ples of water conditioned with nonsterilized, spermiating males (Figs. 3*a*, 3*b*). The isotopic patterns of sterilized and nonsterilized, spermiating males are virtually identical and no other major peaks are present in either spectrum.

Discussion

The combined results of all four experiments show that bisazir-sterilized male sea lampreys during spermiation are capable of attracting ovulating females, and this attraction is mediated through the release of a sex pheromone in an amount similar to that released by nonsterilized males during spermiation. In the first experiment, when placed in a two-choice maze, ovulating females both preferred and spent more time searching in the treatment side of the maze containing chemical stimuli from sterilized, spermiating males. These results are nearly identical to those of Li et al. (2002), where 22 of 22 and eight of eight ovulating females preferred and spent more time searching in the side of the maze conditioned with nonsterilized, spermiating males and 12 of 15 and 7 of 7 ovulating females preferred and spent more time searching in the side conditioned with nonsterilized, spermiating male washings. Searching behavior could be the mechanism underlying the attraction response that leads female sea lampreys to male partners in a spawning stream. Sea lamprey often nest in rapids, and chemical stimuli from nesting animals are flushed downstream (Applegate 1950). Individuals responding to chemical stimuli by searching and swimming against the current stand a better chance of reaching the nesting individuals upstream (Li et al. 2002). Further, ovulating, but not preovulating, females were attracted

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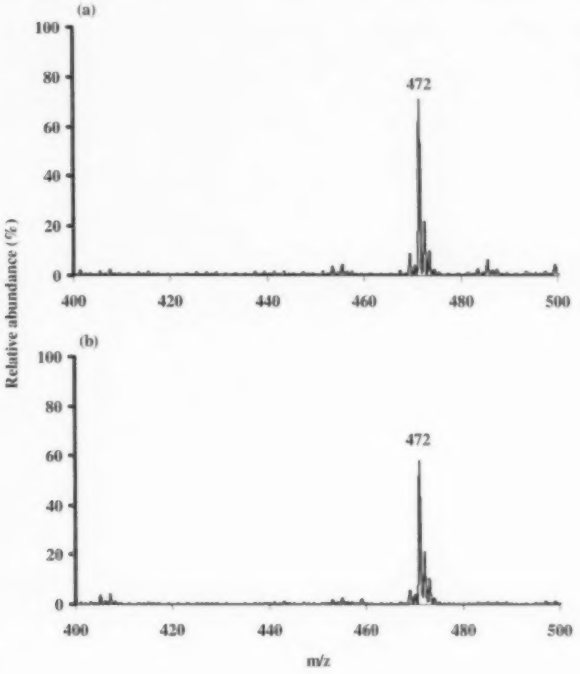
Fig. 3. Negative and positive fast atom bombardment mass spectrometry (10 kV) spectrum of (*a*) extracts of water conditioned with nonsterilized, spermiating male sea lampreys (*Petromyzon marinus*) and (*b*) extracts of water conditioned with sterilized, spermiating males.



to sterilized, spermiating males in their natural spawning habitat, further demonstrating that only ovulating females that are ready to spawn are attracted to spermiating males. It is notable that in a previous study conducted in the same stream section under similar conditions, 9 of 13 ovulating females chose the side conditioned with five nonsterilized, spermiating males (Li et al. 2002), whereas in this study, 10 of 15 ovulating females chose the side conditioned with five sterilized, spermiating males.

The virtually identical levels of behavioral responses observed in the first experiment may be attributable to the virtually identical levels of sex pheromone production and release between sterilized and nonsterilized, spermiating males, as demonstrated in experiments 2 and 3. In the second experiment, EOG results showed that sterilized and nonsterilized, spermiating male chemical stimuli produced similar dose–response relationships in females, demonstrating that the chemical stimuli from both types of animals have the same potency. The olfactory potency of nonsterilized, spermiating male chemical stimuli was first observed by Bjerselius et al. (1995). Our results confirm the potency and show that sterilized males can be just as potent. Also, EOG cross-adaptation experiments showed that chemical stimuli from sterilized and nonsterilized, spermiating males suppressed olfactory responsiveness to each other and to themselves after olfactory adaptation to one had occurred, demonstrating that water conditioned with sterilized and nonsterilized, spermiating males are of the same quality in terms of their olfactory stimulatory effectiveness.

Our fast atom bombardment mass spectrometry analysis further showed that the same pheromonal molecule is responsible for the behavioral and electrophysiological responses elicited by chemical stimuli from both sterilized and nonsterilized, spermiating males. The most abundant molecule contained in extracts of water conditioned with sterilized and nonsterilized, spermiating males has the same molecular weight and isotopic patterns characteristic of 7α,12α,24-trihydroxy-5α-cholan-3-one 24-sulfate, the molecule demonstrated to induce behaviors identical to those induced by nonsterilized, spermiating males (Li et al. 2002) and by sterilized, spermiating males. All four of our experiments demonstrate the biosynthesis and release of a sex pheromone by sterilized, spermiating males. The close similarity of our results to those of Li et al. (2002) also demonstrate that the mechanisms regulating pheromone production and release were intact in males sterilized by bisazir treatment.

For a sterile male release technique to be effective, it is essential that the sterilization process does not negatively affect the mating competency of sterilized individuals (Knipling 1964). Previous field tests demonstrated that sterile male sea lampreys displayed nest-building behaviors and obtained mates (Hanson and Manion 1978). Our study expanded on these findings and further demonstrated that the male sex pheromone signaling system is not affected by bisazir treatment. Bisazir may induce lethal mutations in gametes (Hanson and Manion 1980) that cause premature death in heterozygotes if dominant and in homozygotes if recessive. Spawning behaviors of sea lampreys, on the other hand, are under direct regulation by the central nervous system, which in turn is influenced by the hypothalamus – pituitary gland – gonad axis (Sower 1990). Because the release of sex pheromone coincides with spermiation (Li et al. 2002), a process also regulated by the hypothalamus – pituitary gland – gonad axis (Sower 1990), it is possible that sex pheromone release is also regulated by this axis. It is not likely that the dosage of bizasir injected for sterilization will affect this system and thus reproductive behavior, pheromone release, and ultimately mating efficacy. Further, it appears that the slightly higher than expected levels of egg viability from the sterile male release technique (Bergstedt et al. 2003) is not due to the effect of bisazir treatment on pheromone synthesis and release.

Recently, the potential upregulation of pheromone biosynthesis and release was proposed for the sterile male release technique program of sea lamprey management (Li et al. 2003). The concept is that sterilized males would be induced to synthesize and release the sex pheromone at higher concentrations or for longer periods of time, or both. A similar concept, where cues (similar to natural pheromonal compounds) are synthesized to be more potent, have been developed for the oriental fruit fly (*Bactrocera dorsalis*) and applied in their control (Lanier 1990). If a technique to upregulate the sex pheromone in sea lampreys can be developed, it would potentially improve the efficacy of the current sterile male release technique, which is mainly limited by the number of males that can be collected for sterilization and release (Twohey et al. 2003*b*).

Numerous invasive fish species are currently affecting fish communities in the Great Lakes (Michigan Sea Grant 1994),

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large lake ecosystems worldwide (Hall and Mills 2000), and other aquatic ecosystems across North America (Courtenay et al. 1986). Resistance to widespread use of nonselective pesticides severely limits efforts to control these or any invasive fish species. Also, alternatively, nonchemical control methods have been developed for other pests, but most are not easily transferred to fish. Sterile male release may provide an alternative means to control invasive fish species if it can be demonstrated that bisazir treatment does not affect reproductive function, including production and release of sex pheromones in these fish.

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Predation on stocked Atlantic salmon (*Salmo salar*) fry

J. Nathan Henderson and Benjamin H. Letcher

Abstract: We studied predator–prey interactions between juvenile Atlantic salmon (*Salmo salar*) and trout in three Massachusetts, U.S.A., streams and in artificial streams. We sampled stomach contents of age-1+ and older salmon and trout (*Salvelinus fontinalis*, *Salmo trutta*) following salmon fry stocking in the spring of 1997 and 1998. Between 4.3 and 48.6% of the stocked fry were consumed within the first 2 days after stocking, and total fry mortality from predation varied from 4.3 to 60.7%. No significant differences were found between stomach weights of predators (without fry weight) that consumed fry and those that did not. Artificial stream experiments testing effects of habitat complexity and predator species on predator consumption rates revealed that consumption rates were not different between brook (*S. fontinalis*) and brown (*S. trutta*) trout ($p = 0.59$). Predation rate tended to decrease as the percentage of riffle habitat increased but the decrease was not significant ($p = 0.22$). Our results indicate that predation on stocked Atlantic salmon fry can be substantial (up to 60%), appears to be short lived (2 days), and is not related in a simple way to abiotic and biotic factors.

Résumé : Nous avons étudié les relations prédateurs–proies entre de jeunes saumons de l'Atlantique (*Salmo salar*) et des truites et des ombles dans trois cours d'eau du Massachusetts, É.-U., ainsi que dans des ruisseaux artificiels. Nous avons échantillonné les contenus stomacaux de saumons, d'ombles et de truites (*Salvelinus fontinalis*, *Salmo trutta*) d'âges 1+ et plus à la suite d'alevinages de saumons aux printemps de 1997 et 1998. Entre 4,3 et 48,6 % des alevins ensemencés ont été consommés dans les 2 jours qui ont suivi l'alevinage et la mortalité totale des alevins due à la prédation variait de 4,3 à 60,7 %. Il n'y avait pas de différence significative entre la masse de l'estomac des prédateurs (sans la masse des alevins) qui consomment des alevins et ceux qui ne le font pas. Des expériences en ruisseau artificiel pour vérifier les effets de la complexité de l'habitat et de l'espèce de prédateur sur les taux de consommation des prédateurs indiquent que les taux de consommation ne diffèrent pas chez l'omble de fontaine (*S. fontinalis*) et la truite brune (*S. trutta*) ($p = 0,59$). Les taux de prédation ont tendance à diminuer à mesure qu'augmente le pourcentage d'habitats de rapides, mais cette diminution n'est pas significative ($p = 0,22$). Nos résultats démontrent que la prédation sur les alevins de saumons de l'Atlantique ensemencés peut être importante (jusqu'à 60 %), qu'elle semble limitée dans le temps (2 jours) et qu'elle n'est pas reliée de façon simple aux facteurs abiotiques et biotiques.

[Traduit par la Rédaction]

Introduction

Hatchery-reared fry are often used to restore or replenish depleted Atlantic salmon (*Salmo salar*) runs (Kennedy 1988). In each spring, state and federal agencies stock unfed Atlantic salmon fry into tributaries of the Connecticut River at densities based on stream productivity and fry availability. These fry will remain in the streams for 1–3 years before beginning their migration to salt water. Mortality of stocked fry during their first year is high (Orciari et al. 1994; McMenemy 1995), tends to be density dependent (Whalen and Labar 1994; McMenemy 1995), and can be size selective (Good et al. 2001). Little is known, however, about the actual sources of mortality for Atlantic salmon during their first summer.

The relative importance of predation and starvation as sources of mortality has not been evaluated for Atlantic salmon fry, largely because measuring either source directly is difficult. Letcher and Terrick (2001) found very high mortality rates for stocked fry that were held in the hatchery beyond a certain point. Laboratory studies indicated that these fish most likely died from starvation after about 4 days in the stream. Starvation for fish stocked following a more typical number of days in the hatchery was unlikely and would have

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taken about 20 days if fish had no access to food. It appears that starvation is not typically a major source of mortality for Atlantic salmon fry.

Predation has the potential to be a major source of mortality for stocked fry because predators and prey overlap in space and time, fry are small enough to be consumed by most of the possible predators, and fry are introduced rapidly into a novel environment. Despite the potential importance of predation on fry, Mather (1998) found that no studies have been conducted to assess the importance of predation on fry, although brook trout (*Salvelinus fontinalis*; McCrimmon 1954; Symons 1974), brown trout (*Salmo trutta*; Brannas 1995), and Atlantic salmon parr (Pepper et al. 1985) are known to consume stocked fry. Additional anecdotal information also suggests that predation on stocked fry by resident salmonids could be high (McCrimmon 1954; Symons 1974; Pepper et al. 1985).

Our goal was to determine the extent of predation on stocked fry by estimating the percentage of stocked fry consumed by resident predators in a variety of habitats. We conducted stomach analyses of predators following fry stocking in three rivers that varied in densities and species of possible predators. We also evaluated the time course of predation following stocking with sequential sampling of replicate plots and conducted an artificial stream study to evaluate directly the effect of habitat on predation by brook and brown trout.

Methods

Study areas

The study area included three streams in western Massachusetts (approximately 42°35′N, 72°45′W): the North Branch of the Manhan River (MR), Four Mile Brook (FMB), and Mill Brook (MB). The study reaches are stocked annually (36–89 fry·100 m^{-2}) by state and federal agencies with unfed Atlantic salmon fry. The study reaches were chosen to target fish assemblages where salmon co-occur with one or two trout species.

The MR supports a natural brown trout population that is supplemented annually with hatchery brown, rainbow (*Oncorhynchus mykiss*), and brook trout. The MR can be characterized as a low-gradient stream where pools dominate the available habitat (Table 1). The FMB is a moderate-gradient stream with riffle habitat as the predominant habitat type, but woody debris creates complex pools providing ample trout habitat (Table 1). The FMB supports a natural brook trout population, which is supplemented annually with stocked hatchery brook trout. The MB is a moderate-gradient stream with both riffle and pool habitat equally available (Table 1). The MB supports naturally reproducing brook and brown trout and is also stocked annually with hatchery brook and brown trout.

FMB and MB have a broad range of mixed deciduous and coniferous trees contributing to the riparian canopies. A mix of pastureland and coniferous trees dominates the MR. All study streams were second to third order, and study sites were designed to contain 80 units of 100 m^2.

Field study

Predator densities before fry stocking

Electrofishing is known to affect short-term fish behavior (Mesa and Schreck 1989); therefore, initial predator population estimates were conducted at least 1 week before fry stocking. Because of flooding conditions in 1998, population estimates in FMB were obtained after fry stocking. Fish were collected using a Smith-Root backpack electrofishing unit (500 V DC, unpulsed; Smith-Root Electrofishing Co., Vancouver, Wash.). The abundance (± standard error (SE)) of each predator species was estimated using the three-pass removal method (Bohlin et al. 1989). Each reach was sectioned into 80 units of 100 m^2, and fish sampling was conducted in randomly selected units making up 20% of the available habitat within the reach. The selected units were blocked off at the upper and lower ends with a mesh net that prevented fish from escaping the area. All resident salmonids were measured (total length and fork length (FL)) to the nearest millimetre and weighed to the nearest 0.1 g and then returned to the areas from which they had been removed.

Fry stocking

Fry (FL ± standard deviation (SD) = 26.2 ± 1.4 mm) were stocked in the study reaches in 1997 and 1998 approximately between 1000 and 1100. We poured fry from white buckets throughout the stream by the standard scatter–plant method used by state and federal agencies. This method is designed to evenly distribute fry into suitable riffle habitats. In 1997 and 1998, fry densities of 59 and 70 individuals·100 m^{-2} were stocked in the FMB and the MR, respectively. Densities inside study sites matched densities of fry stocked by state and federal agencies outside study sites. Fry stocked outside study sites were stocked on the same day and at about the same time as study site fish. In 1997, MB was stocked with 52 fry·100 m^{-2}. Because of weather conditions in 1998, fry were planted by state agencies in the MB a week ahead of schedule; consequently, it was not used as a study stream in 1998.

Predator sampling after fry stocking

Predators were sampled by electrofishing 1 h after stocking, at dusk, and at midnight of the day of stocking to determine if diel activity of the predators and prey affected predation rate. Additional sampling was conducted 1, 2, 3, 5, and 7 days after stocking between 0600 and 1000. Thereafter, weekly sampling was conducted for up to 1 month after the date of stocking. Because electrofishing may adversely affect the stream community, all sampling was conducted in separate sections of the stream. Each sample was divided into a sample block. Sample blocks consisted of five contiguous units, four of which were sampled in a downstream-to-upstream fashion to avoid capturing predators that consumed prey items dislodged during sampling. The top unit was skipped, which avoided directly affecting behavior of predators and prey in the next upstream reach. Units for the next sample were located directly upstream of the previous sample block.

Incidence of predation

Potential predators were removed from the stream and measured for total length (±1 mm) and weight (±0.1 g).

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Table 1. Physical characteristics of the study streams.

Stream	Wet width (m, mean ± SD)	Depth (m, mean ± SD)	Gradient (%)	Pool habitat (%)	Riffle habitat (%)
Four Mile Brook	4.7±1.4	0.17±0.08	2	35.4	64.6
North Branch of Manhan	8.6±1.2	0.53±0.01	1	58.2	41.7
Mill Brook	6.6±1.4	0.13±0.02	1	57.3	42.7

Note: Data collected in the fall of 1998. SD, standard deviation.

Predators were anesthetized with clove oil (Anderson et al. 1997), and stomach contents were removed by gastric lavage (Light et al. 1983). All stomach contents were preserved in 95% ethanol. Most predators were released after gaining equilibrium; however, 15 fish from each stream were sacrificed and the remaining stomach contents were identified. From this sample, we determined that 3% of the prey items were missed by the gastric lavage technique. All fry positively identified as salmon fry were within the narrow range of sizes of stocked fry (24–28 mm).

Alternate prey sampling

Prey availability for salmonids has been commonly defined by the amount of drifting invertebrates (Allan 1978; Rader 1997). We collected drifting invertebrates (drift nets, 125 μm mesh, 30 cm × 30 cm wide; Allan and Russek 1985) in the FMB and MR in the spring of 1998 during each sampling date to determine if prey availability in the drift affected predation rates on fry. Single drift samples were collected above electrofishing areas at the conclusion of predator sampling. Each net was >6 cm from the bottom of the stream substrate, and the top of the net always extended above the water surface. Water velocity ($m \cdot s^{-1}$, Marsh and McBirney portable water current meter; Marsh and McBirney Inc., Frederick, Md.), and water depth (cm) were recorded at the water surface. The duration of individual drift samples ranged from 20 min to 1 h depending on stream conditions.

Benthic organisms were collected using a Surber sampler (Wildlife Supply Co., Buffalo, N.Y.) (0.55 mm mesh) at the conclusion of predator sampling. Samples were taken randomly in replicate pairs both in a pool and in an adjacent riffle. Invertebrates in the drift and benthos were preserved in 95% ethanol and later sorted in the laboratory.

Abiotic factors

A permanent station was chosen in each stream from which to sample various abiotic variables. Stream discharge ($m^3 \cdot s^{-1}$) was estimated by using a measure of the average stream velocity and cross-sectional area. Flow for this calculation was measured using the portable water current meter. After a stage–discharge relationship was developed across a wide range of discharge levels, the discharge was determined simply by monitoring the water level. Temperature was measured with a temperature logger (2-h intervals), and turbidity (nephelometric turbidity units, NTU) was determined from daily water samples.

Laboratory analysis

All stomach content samples were rinsed, rehydrated, and examined under a dissecting microscope. Rates of gastric evacuation for trout (Elliott 1991) allowed us to identify with confidence all fry up to 6 h after consumption. All possible fry were compared with reference samples collected on the day of stocking to compare size, weight, and morphological characteristics. Any questionable fish were not included in the analysis. Invertebrates were identified (to family level) and were enumerated by counting only head capsules. Stomach samples were then dried at 75°C for 48 h. Dry weights were measured to the nearest 0.1 mg.

Organisms in drift samples were enumerated and taxa were identified to the family level (Merritt and Cummins 1996). All organisms in Surber and drift samples were removed and split using a plankton splitter. Larger samples required a reduction to 25%, and one of every five split samples was measured entirely to ensure homogeneity among each split. Abundance of organisms was determined in both drift and benthic samples by estimating the number of organisms in each sample per total flow (drift) and unit area (benthic).

Artificial streams

We tested the hypothesis that habitat type (pool-to-riffle ratio) influences predation on stocked fry in 12 artificial stream sections in outdoor raceways at the Richard Cronin National Salmon Station, U.S. Fish and Wildlife Service (USFWS), Sunderland, Mass. The streams were designed in a seminatural environment that allowed for control of flow, emigration, immigration, avian predation, habitat, and prey–predator densities and size ratios. The streams were constructed in three existing 30.5 × 4.5 m raceways. Water entered the artificial streams by a gravity-fed system and was classified as an open system (once-through flow with complete exchange) (Lamberti and Steinman 1993).

We tested the prediction that habitat complexity reduces predation on stocked fry by means of a completely randomized design with equal treatment densities (number of fry per stream). Each raceway was divided into four equally sized stream sections for a total of 12 sections. Sections were designed with differing pool-to-riffle ratios. Habitat 1 was a 75% pool (3:1 pool-to-riffle ratio), habitat 2 was a 50% pool (1:1 pool-to-riffle ratio), and habitat 3 was a 25% pool (1:3 pool-to-riffle ratio). Each habitat type was situated randomly within the three raceways. Depth, velocity, substrate, and cover were replicated and were analogous to those commonly used by both predator species in the wild (Heggenes 1988; Heggenes and Saltveit 1990). Pools were 20–25 cm in depth, and boulder edge was the dominant cover type. Riffles were about 5–7 cm in depth and had equal mixture of 2–7 cm gravel and 13+ cm cobble substrates. Each stream section was separated by a 0.31 cm mesh block gate. This prevented both predators and fry from escaping the stream section, and 22 mm mesh nylon netting was secured over each stream section to exclude avian predation.

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Stocked fry

Atlantic salmon fry of sea-run parentage were obtained from White River National Salmon Hatchery (USFWS, Bethel, Vt.) and placed in controlled-temperature hatching trays. Because trials were run over the course of almost 1 month, we adjusted the development rate of fry for stocking so that developmental stage was the same for all fry. The fry for each trial were incubated to a developmental index (DI (± SE), Kane 1988) of 93.2 ± 0.2 and left unfed, which is the standard protocol for stocking. Adjusting the ambient temperature in each hatching tray controlled fry development for fish from different trials.

Predators

Native brook trout captured in adjacent stream channels and hatchery-raised brown trout were used as the predator species. All predators were brought to the hatchery and placed in holding tanks 34 days before the first experiment. Each week we randomly introduced six trout of the same species into each stream unit 4–5 days before an experiment began. Four small size class fish (150–185 mm FL) and two large size class fish (195–220 mm) were introduced into each stream unit. These numbers and sizes were representative of those observed among wild populations in the field.

Trials

Each trial used 12 stream units (two species × three habitats × two replicates). In total, five experiments were conducted between 11 March and 7 April 1998. Thirty-three fry were evenly stocked into each stream unit. The stocking density was similar to stocking densities in the wild. Predators were removed 1 h after fry stocking by backpack electrofishing. This time frame was chosen because preliminary data collected in the field in 1997 indicated that most fry predation occurred 1 h after stocking. After electroshocking, predators were anesthetized with tricane methanesulfonate (100 $mg \cdot L^{-1}$), measured for length (mm), and weighed (0.1 g). Stomach contents were removed by gastric lavage and preserved in 70% ethanol, and the number of fry consumed by each fish was determined later in the laboratory.

Data analysis

Field study

We report incidence of predation as both the percentage of stocked fry following stocking and as the percentage of total mortality from survival estimates in the fall. These estimates were conducted by fall electrofishing surveys. Number of fry eaten per unit was calculated as the number of predators multiplied by the mean number of fry per predator and was divided by the number of fry stocked (percentage of fry stocked) or by the estimated mortality (numbers, percentage of total mortality).

Fry positively identified in stomach contents were enumerated and expressed as a percentage of all stomachs (Hyslop 1980).

$$(1) \qquad \frac{\text{no. of stomachs with fry}}{\text{no. of stomachs}} \times 100$$

Stomach samples were analyzed for mean specific dry weight (g) to compare differences in the gut weight of predators at the time of stocking. A ratio of dry weight of stomach content to fish wet weight was created using

$$(2) \qquad \frac{\text{stomach content dry weight}}{\text{fish wet weight}} \times 100$$

to allow for comparison across size classes. These data were pooled across sites and compared by species using Duncan's multiple range test. Fry dry weight was expressed as a percentage of the overall dry weight of the stomach to determine the specific contribution of fry to the diets of the predators.

We used invertebrate density as a measure of food abundance from the benthos and drift. Densities per litre in the drift were calculated using (Allan and Russek 1985)

$$(3) \qquad \frac{\text{no. per net-hour}}{\text{litre filtered per net-hour}} \times 100$$

Similarly, benthic prey density was estimated for each site as the number of organisms sampled per square metre.

We used multiple regression analysis to explore the relationship between the response variable, the number of fry eaten, and multiple predictor variables. Because there are yearly stream and temporal effects, we only assessed within stream patterns for data collected in 1998. We used the SS3 option in the general linear model (PROC GLM, SAS Institute Inc. 1990) that utilizes a type III hypothesis and makes the order of variables entering in the model statement not significant.

We used principal component analysis (PCA) solely for descriptive purposes to explore major gradients of variation in the gut contents among fish within a species that consumed fry and those that did not. PCA was used to reduce the dimensionality of the variables (number of prey items) in the guts of predators to a smaller number of principal components. These dominant gradients were summarized, and observations on individual fish were compared by their location (PCA scores) on the first few composite dimensions. Stratification by sample time was used to reduce temporal variation in invertebrate abundance. The data were tested for assumptions of univariate and multivariate normality. In most cases, multivariate normality was not met; however, concern over meeting assumptions of normality is not generally warranted in ecological research when using PCA for descriptive purposes.

Artificial streams

Analysis of variance (ANOVA) was used to examine the effects of habitat type, predator species (brook and brown trout), and predator size on fry predation. The full model was reduced to main effects because higher-order interactions were not significant. The reduced model examined how predation varied with differences in species composition and habitat type and was applied to data from all weeks. The Tukey's honestly significant difference (HSD) test was used to identify differing groups.

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Results

Field study

Predator densities before fry stocking

Despite great variation at individual stream units, the average density of predators was similar from year to year among rivers (Fig. 1). Population estimates of total salmonid predator abundance averaged (±SD) 17.2 ± 3.5 (FMB), 10.8 ± 1.3 (MR), and 3.3 ± 1.6 (MB) fish·100 m^{-2}. The MB was dominated by brook trout, the FMB contained similar densities of Atlantic salmon and brook trout, and the MR had either equal densities of Atlantic salmon and brown trout (1997) or greater numbers of brown trout (1998, Fig. 1). In all streams, small size class fish (0–100 mm) were the most abundant and averaged (±SD) 2.6 ± 2.9 fish·100 m^{-2}. Large size class fish (>130 mm) were the least abundant and averaged 1.1 ± 1.2 fish·100 m^{-2}.

Predator sampling after fry stocking

During the entire study, we captured 843 predators of four salmonid species: Atlantic salmon, brook trout, brown trout, and rainbow trout. In 1998, large rainbow trout (FL >300 mm) were stocked into the MR about 5 days before fry stocking and consequently had not been found during population estimates. Mean size and minimum size of predator individuals varied by species (Table 2). Overall, brook trout were the most common species and large rainbow trout were the least common.

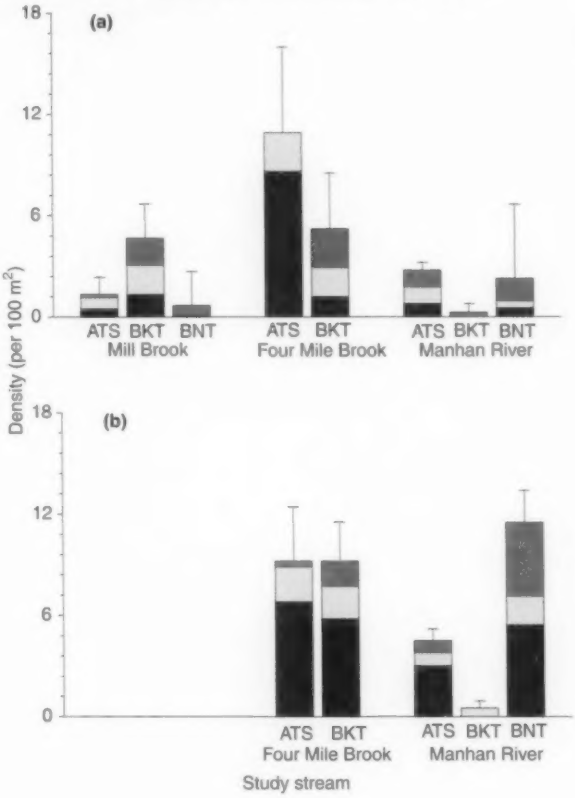
Incidence of predation

It was possible to positively identify 100% of the fry consumed by predators as Atlantic salmon fry after the first day; thereafter, 73% of the fry were readily identifiable. Fish that were too digested to be confidently identified were not included in subsequent analysis. In both years, predators were observed to consume fry in each stream (Fig. 2). All observed occurrences of fry predation were within 2 days of stocking. The majority of predation was found to occur within the first day (4.3–44.3% of stocked fry). At least one predator was observed to consume a fry 1 h after stocking in each year and each stream. The percentage of fry stocked that was consumed 1 h after stocking ranged from 4.1% in the MR to 24% in the FMB (Fig. 2). Total percent predation was variable among streams and was greatest in the FMB (48.6%) in 1998 and lowest in the MB (4.3%).

Over the course of the entire sampling, 5.3% of the predators observed had consumed fry. In 1997, brook and brown trout were the only predators observed to consume fry (Table 2). In 1998, all four salmonid species consumed fry. The number of fry in the guts of predators ranged from 1 to 8. A brook trout of FL = 78 mm was the smallest, and a rainbow trout of FL = 340 mm was the largest predator observed to consume fry. Within the first 3 days, 15% of the brook trout and 11% of the Atlantic salmon parr captured in the FMB in 1998 had consumed fry (Fig. 3). In 1998 in the MR, this estimate ranged from 2% of the brown trout to 14% of the rainbow trout. In 1997 in the MR, 50% of the brown trout and 25% of the stocked rainbow trout contained fry after 1 h.

In the fall, population estimates were conducted to determine survival of age-0 fry from fry stocking. This estimate was used to calculate the overall percentage of mortality resulting from predation (Table 3). In 1998, 60.7% of total fry mortality to the first fall could be accounted for by predation in the FMB. In the MR this estimate ranged from 11.3% in 1997 to 13.1% in 1998. Overall, there was no relationship between fry survival to the first fall and the rate of predation ($p = 0.16$).

Fig. 1. Density (no.·100 m^{-2}, mean ± standard error) of predators in (*a*) 1997 and (*b*) 1998 before Atlantic salmon (*Salmo salar*) fry stocking in the three study streams. Mill Brook in 1998 was not included in the analysis. Predators are shown in three size classes: solid bars, <<100 mm; open bars, 101–130 mm; shaded bars, >131 mm. ATS, Atlantic salmon (*S. salar*); BKT, brook trout (*Salvelinus fontinalis*); BNT, brown trout (*Salmo trutta*).



Alternate prey sampling

The density of drifting and benthic invertebrates varied widely over the day and night. The diel periodicity of total drift followed the typical pattern of higher numbers at dusk than at dawn. The production of benthic prey was characterized by large differences in density per stream section. Overall, FMB had higher densities of both benthic and drifting prey items and was dominated by species in the orders Ephemeroptera and Collembola. MR was dominated by prey in the order Collembola and species in the families of Chironomidae and Ephemerellidae.

Gut content analysis

Throughout the study, only 6% of the predators were found with empty stomachs, indicating that most fish were

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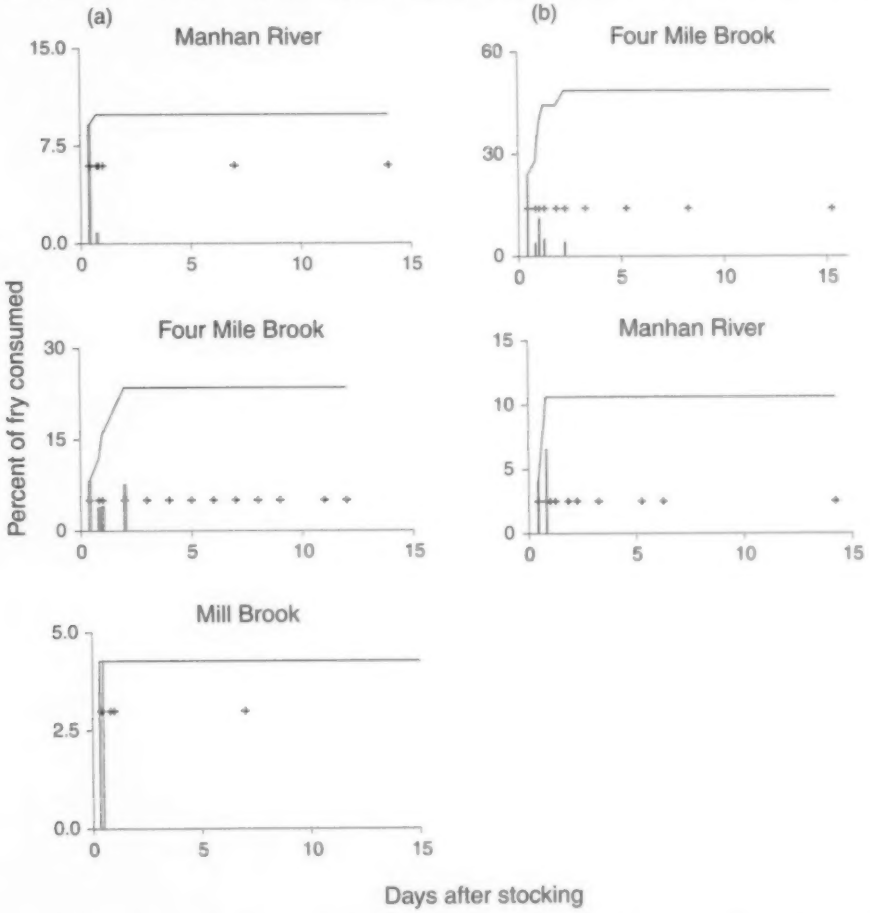
Table 2. Summary of predator fork length (FL) and range of fry numbers consumed per predator in 1997 and 1998.

Year	River	Species	Predation by species (%)	Range of fry	FL (mm)		
					Smallest predator	Largest predator	Mean of all predators
1997	Manhan River	Brown trout	100	1–6	138	202	164
	Four Mile Brook	Brook trout	100	1–2	104	215	158
	Mill Brook	Brook trout	100	1	142	220	166
1998	Manhan River	Brown trout	55	1–2	169	192	201
		Rainbow trout	45	1–4	340	340	340
	Four Mile Brook	Brook trout	60	1–8	78	162	101
		Atlantic salmon	40	1–5	80	123	94

Fig. 2. Percent of stocked Atlantic salmon (*Salmo salar*) fry consumed over time in the Manhan River, Four Mile Brook, and Mill Brook in (*a*) 1997 and (*b*) 1998. Bars represent percent fry consumed; solid lines, cumulative percent predation; +, sample time.



actively eating. On the average, brook trout stomach contents weighed twofold more than Atlantic salmon stomach contents in the FMB. In the MR and MB, mean specific gut masses were not significantly different among species in 1997. In 1998 only rainbow trout gut masses were significantly lighter (p = 0.008) compared with those of other salmonids. Mean specific gut masses (without weight of fry) of fish consuming fry were not significantly different from those of fish that did not consume fry (Duncan's multiple range test, p = 0.38). The overall contribution of fry to the diets of predators that consumed fry (fry dry weight divided by stomach content dry weight) varied among species and ranged from 1 to 86% during the sample period.

Because we observed major spikes in invertebrate abundance, patterns were only assessed for an individual sample time and species. PCA was used to reduce the major prey categories (orders of invertebrates) down to a smaller number of principal components (PC). The patterns in these anal-

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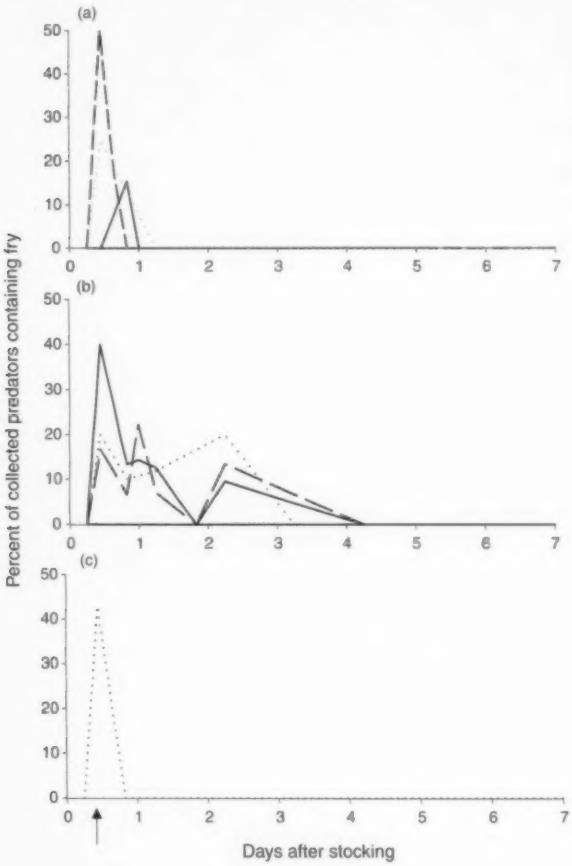
Fig. 3. Percent of collected predators containing Atlantic salmon (*Salmo salar*) fry over time in (*a*) Manhan River (broken line, brown trout 1997; solid line, brown trout 1998; dotted line, rainbow trout 1998); (*b*) Four Mile Brook (dotted line, brook trout 1997; solid line, Atlantic salmon 1998; broken line, brook trout 1998); and (*c*) Mill Brook (dotted line, brook trout 1997). Arrow indicates the time when Atlantic salmon were stocked. Data shown are for the first week after stocking fry.



yses indicated that all predator species did not tightly cluster to the gradients (invertebrate orders) defined by the PC in each analysis, and neither predators that consumed fry nor those that did not were strongly selecting among different invertebrate orders.

Abiotic factors

Abiotic factors were variable among years and streams during the sample period. For example, in 1997 flow during the sampling times in the FMB averaged 0.48 $m^3 \cdot s^{-1}$, which was two times greater than in 1998 (0.19 $m^3 \cdot s^{-1}$). Temperatures in 1997 were 1.3°C cooler than in 1998. These trends were similar to those in the MR, where temperature in 1997 was 3.0°C cooler than in 1998 and flow in 1997 averaged 1.28 $m^3 \cdot s^{-1}$ and in 1998 averaged 0.79 $m^3 \cdot s^{-1}$. Abiotic factors in the MB and MR were very similar 1997: flow averaged 1.12 $m^3 \cdot s^{-1}$ and temperature averaged 7.8°C.

Multiple regression model

We used multiple regression techniques to explore the relative importance of various predictor variables on the response variable number of fry consumed per predator. Because all fry predation occurred within the first 3 days after stocking, the models were constructed using data from this time frame. Each predictor variable was assessed for collinearity, and pairs of variables with high R^2 were removed from the analysis. The variables that were retained in the model included total discharge, turbidity, average temperature, predator FL, weight specific dry weight (stomach contents), total drift density, and total benthic numbers·m^{-2}.

Fry consumption was significantly related ($p = 0.0009$) with the combination of variables in the FMB when all predators (brook trout + Atlantic salmon) were included (Table 4). Predator FL and the percentage of riffle habitat were positively related to the number of fry consumed, whereas total drift was negatively related. Despite p values < 0.05, the full model only explained 11% of the variation in predation rate.

In the FMB, weight-specific dry weight of gut contents for Atlantic salmon predators was identified as an important independent variable for fry consumption. This relationship was positive; eating more in general also resulted in an increased number of fry consumed. FL was positively related to the number of fry consumed, whereas drift was negatively related to the amount of fry consumed. In the MR, the full model was not significant; however, average FL of all predators was positively related ($p = 0.005$) to fry consumption.

Artificial streams

Predation trials

Overall, 6.5% of the stocked fry were eaten during the five experiments. No dead or injured fry were observed; therefore, we assumed that predation was the only source of mortality. Average temperature during the trials was 8°C. In addition to fry, trout stomachs were commonly observed to contain invertebrates in the families of Simulidae and Centropogonidae. Thirty-two percent of the predators had empty stomachs and 10.3% had eaten fry. Brown trout (n = 36) consumed 2.8% of the stocked fry, and brook trout (n = 28) ate 3.6%. Brook trout predation decreased from 8.9% in habitat 1 to 3.6% in habitat 3 (Fig. 4). Brown trout predation was more variable and was greatest in habitat 2 (12.1%). Small size class brook trout consumed 1.6% of the stocked fry, and small size class brown trout consumed 2.3%.

Differences between and among the two species and all main effects and interactions for size class were not significant (ANOVA, $F = 0.36$, $p = 0.50$); therefore, size classes were pooled. In the full model, the number of fry consumed did not differ from week to week ($F = 0.8$, $p = 0.57$). The full model was reduced to include only main effects and two-way interactions. In the reduced model, there were no significant effects of species ($F = 0.07$, $p = 0.73$) or habitat type ($F = 2.37$, $p = 0.09$) on predation rates. Despite a marginal effect of habitat type on predation rates, there was a general trend of decreasing predation rate by brook trout as the percentage of riffle habitat increased (Fig. 4).

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Table 3. Times of stocking and percentage of overall mortality that could be accounted for by predation.

Year	Stream	Date stocked	Fry stocked (no.·100 m^{-2})	Stocked fry consumed (%)	Fry in the fall (no.·100 m^{-2})	Estimated survival to fall (%)	Mortality from predation (%)
1997	Manhan River	10 April	70	11.2	10.6	15.1	13.2
	Mill Brook	23 April	52	4.3	5.7	11.0	4.8
	Four Mile Brook	19 May	59	23.5	10.3	17.5	28.5
1998	Manhan River	8 April	70	10.7	13.1	18.7	13.1
	Four Mile Brook	19 May	59	48.6	9.2	20.0	60.7

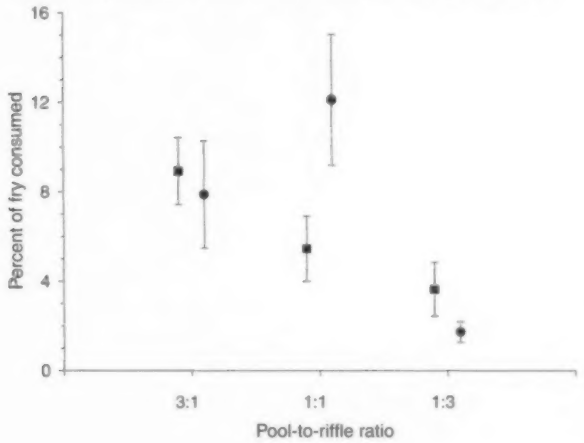
Note: Percentages are derived from survival estimates in the fall.

Table 4. Results from multiple regression models to determine the relative importance of various predictor variables on the response variable, the number of fry consumed.

Stream	Model	Mean no. of fish · 100 m^{-2}	R^2 (full model)	P (full model)	Significant predictor variables	df	MS	F	P	Correlation estimate
Four Mile Brook	All predators	18.4	0.112	0.0009	Fork length (mm)	1	4.32	5.83	0.009	0.006
					Riffle habitat (%)	1	2.71	4.29	0.004	0.036
					Drift (no.·L^{-1})	1	4.12	6.63	0.011	−15.28
	Atlantic salmon	9.2	0.083	0.204	Gut weight (%)	1	2.21	3.99	0.049	0.35
	Brook trout	9.2	0.154	0.01	Fork length (mm)	1	4.14	5.82	0.017	0.007
					Drift (no.·L^{-1})	1	7.78	10.93	0.001	−32.88
Manhan River	All predators	16.5	0.07	0.176	Fork length (mm)	1	0.74	3.71	0.005	0.0012
	Brown trout	9.6	0.04	0.878	None					
	Rainbow trout	1.3	0.095	0.263	None					

Note: Only significant ($p < 0.05$) predictor variables are shown for each model. Models were only constructed for year 1998. df, degrees of freedom; MS, mean square.

Fig. 4. Percent (mean ± standard error) of Atlantic salmon (*Salmo salar*) fry consumed across habitat types during the 5-week artificial stream experiment: solid squares, brook trout (*Salvelinus fontinalis*); solid circles, brown trout (*Salmo trutta*).



Discussion

Our results suggest that piscivory can be short lived but very intense and can impose significant mortality on fry. In both years in the field and in the artificial streams, stocked Atlantic salmon fry were consumed by resident salmonids. Among streams, predators ate 4 to 49% of stocked fry during the first 2 days after stocking. The percentage of total mortality resulting from predation from spring stocking to the fall sample varied between 4.8 and 60.7% among streams. All predation events occurred within a 2-day period, indicating that predation on fry may be quite short lived. In streams like the MR and MB, where predation accounted for only 4.8 and 13.2%, respectively, of the overall mortality to the first fall, factors other than predation accounted for most of the mortality. However, under certain circumstances, such as in the FMB where resident salmonids were abundant, predation can be a substantial source of total mortality.

Predation and mortality rates on stocked fry in our study were likely underestimated. We used a conservative criterion to discriminate Atlantic salmon in the guts of predators. Overall, 6.4% of the fish found in the stomachs of predators were not easily identifiable and subsequently were not included in the analysis. If these unidentifiable fish were in fact Atlantic salmon fry, our estimates of mortality from predation in 1998 would have increased from 60.7 to 67% in the FMB and from 13.1 to 22% in the MR. This problem was minimized somewhat by the frequent sampling during the first 24 h after stocking but could have become larger during the subsequent days and weeks after sampling because sampling was confined to 0600 to 1000. Any dusk-to-midnight predation would not have been recorded because of our conservative identification criteria.

Predation on fry may also have been underestimated because we simply counted fry in the guts of predators and did not adjust the counts to a full day of consumption. Counts could be adjusted using evacuation rate methods (Bromley 1994) or a bioenergetics model (e.g., Hansson et al. 1996). Individual predators could have eaten more fry during the course of the day than our counts indicated, resulting in increased fry consumption estimates. Combining an evacuation rate model (Elliott and Persson 1978) with evacuation rate estimates for brown trout feeding on fish (He and

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Wurtsbaugh (1993), temperature = 8°C and prey size = 0.02 g) indicated that predators could have consumed 62% more prey over 12 h than indicated by our counts. This estimate assumes that predators were eating constantly during the 12 h. Because the extent to which our predators consumed fry continuously during the day was unknown, we opted to estimate predation rates conservatively based on counts alone, but they almost certainly underestimate actual full-day predation rates.

Another potential source of bias in our predation rate estimates is emigration of stocked fry out of our study sites. Emigration could affect both our short-term estimates of the percentage of stocked fry that were eaten and the longer-term estimates of the percentage of mortality accounted for by early predation. Stocked or emerging fry tend to disperse over short time scales before setting up territories (McCormick et al. 1998). This movement could cause an underestimate of the actual percentage of fry eaten if fry that emigrated from study sites were not replaced by immigrants. Because our study sites were nested within steams that were stocked at the same time from the same source of fish as the study sites and there is no reason to suspect that the probability of moving in and out of sites would be different, we believe that emigration out of study sites probably did not influence our predation estimates. Permanent emigration without replacement over longer time scales (stocking to the fall sample) could also result in an underestimate of survival probabilities and, consequently, an underestimate of the percentage of mortality from predation. In previous studies on nearby streams (Letcher and Terrick 2001), about 60% of the fish captured in study sites had been stocked in study sites; there was no difference in study site retention rates among streams and no differences in densities in or out of study sites. These observations suggest that movement from stocking locations in Massachusetts streams certainly does happen, but that immigration may be balanced by emigration over small spatial scales (100 m), making it unlikely that movement during age 0+ causes a substantial bias in survival estimates.

The existence of movement within the streams for age-0+ fish may also be related to the lack of correspondence between predation and survival across streams. Locally high predation rates may be compensated for by immigration into depleted areas. The short-lived nature of the predation that we observed on stocked fry and the lack of a longer-term effect on survival estimates suggest that early predation, although it can be intense in some systems, may not be a controlling factor regulating Atlantic salmon production in small streams.

Resident salmonids are found in nearly all streams that are stocked with Atlantic salmon fry. In this study all salmonid species were observed to consume fry. For this reason predation rates may be difficult to predict because of the complexities of inter- and intra-specific interactions. Larger brown trout are piscivores (Shetter and Alexander 1970), and of the salmonid predators, we speculated that they would consume a greater proportion of stocked fry. In contrast to this idea and similar to observations by McCrimmon (1954), brook trout consumed the most fry in the field and in artificial streams. McCrimmon (1954) further suggested predation by large brown trout and rainbow trout could have greater impact on larger parr than on fry. Because our study was only conducted intensively in the first month after stocking, predation rates by these larger species may also be important later. There is little information on predation rates by resident salmonids on salmon parr; acquiring this information may be especially important in streams such as the MR because of the high density of large brown trout.

In this study, brook trout consumed the most fry in the field and in the artificial streams. In order to co-exist when resources are limiting, individuals must partition the stream environment. Brook and brown trout occupy a wide range of habitats (Baker and Coon 1997) and in allopatry occupy similar habitats (Fausch and White 1981). Larger brook and brown trout occupy midstream cover and utilize more of the available habitat, whereas smaller fish tend to occupy faster-moving areas. Brown trout, however, tend to hold position in deep holes more frequently than brook trout (DeWald and Wilzbach 1992). As a consequence, smaller brook trout may increase their chances to encounter and effectively intercept fry because of their presence in riffle sections.

There are many sources of variation in predation rates including density of predators, prey and predator size, alternate prey, behavior, habitat utilization, and abiotic factors. The density of predators and prey affects predation intensity. Mills (1969) concluded that Atlantic salmon survival was both density dependent and dependent on the density of older fish such as salmon parr and brown trout. Increased predator density can also increase the mortality of a constant number of salmonid prey (Beauchamp et al. 1995). The density of predators in our study was higher in 1998, which may partially explain the higher predation rates in that year. Prey numbers can also affect the outcome of predation (Mather 1998). In Massachusetts, fry stocking densities are based on fry availability and stream productivity. Consequently there is yearly variation in fry stocking densities among streams. The stocking densities in our study were fixed. However, changes in stocking densities and how they relate to the extent of predation deserve attention.

Stream salmonids are predominantly visual predators (Gregory and Levings 1998), and as a defense mechanism, prey often use cryptic coloration to avoid predator detection (Donnelly and Whoriskey 1993). In our study cryptic coloration was not measured; however, fry were observed to match the color of the white buckets during stocking. Donnelly and Whoriskey (1993) found fry that were not color acclimated to a stream experienced higher rates of predation after stocking. Also, before stocking, fry have never experienced a threat of predation. Metcalfe et al. (1987) found that Atlantic salmon, after experiencing a predator attempt, modified their behavior in ways that made attacks less likely. These observations are consistent with our findings that predation on fry occurred mainly in the first 2 days after stocking and suggest that further study on ways to minimize chances of early predation may be useful. It would be interesting to evaluate the effects of stocking from dark buckets or possibly at night on the extent of predation on fry.

In the face of a changing environment and intense competition, most fish species depend on some level of opportunism for survival. Although drifting prey may be an important component of stream salmonid diets, the importance of scarce large items such as terrestrial prey are poorly understood (Poff and Huryn 1998). In our study fry constituted a small

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portion of the overall diets of predators. The overall significance of rare events to predator growth and survival, such as fry stocking, is difficult to determine. We did not find differences between the stomach weights of predators (without fry weight) that consumed fry and those that did not. Consequently, predators do not appear to be consuming fry as a result of hunger, rather as a result of opportunity. This may explain why all predators were not consuming large prey items such as fry.

For a predator to take advantage of a profitable prey item, both prey and predator must overlap in time and space. Stocking fry in Massachusetts streams occurs over a 2-month period starting in April. Spring months have been demonstrated to be an important time for trout and salmon foraging (Needham 1930). In early April, stream temperature and food resources may be lower than later in the spring. Elliott (1975) found that consumption rates for brown trout were significantly lower when temperatures were less than 6°C and were maximal between 13 and 19°C. At the time of stocking, stream temperatures averaged 6–8°C higher in the FMB than in the MR and MB. If the MB and MR had been stocked when stream temperatures were higher, when brown trout are known to increase food consumption, predation rates in these streams could have been higher.

Many biotic and abiotic factors combine to influence the survival of Atlantic salmon in their first year. Our study demonstrated that over 50% of the first-year mortality could be explained by predation alone, but that the relative importance of predation mortality varied substantially among streams. However, the timing of predation mortality was consistent across all streams; all predation mortality on stocked fry occurred within the first 2 days after stocking. The short-lived nature of predation mortality and its variation among systems indicate that the overlap between local conditions in the stream (flow, temperature, species composition, habitat, etc.), varying conditions of the fry (density, developmental stage, fry condition, and coloration), and the timing of stocking could interact in very complex ways to determine the extent of predation on fry. The small amount of variation in predation rates explained by our multiple regression analysis reinforces the complex relationship between fry predation and the independent variables. Although the relationship among variables responsible for structuring the extent of fry predation may be difficult to explain, we have shown that fry predation, in certain situations, can represent a substantial amount of the variation in fry survival.

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Changes in phytoplankton communities following logging in the drainage basins of three boreal forest lakes in northwestern Ontario (Canada), 1991–2000

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Abstract: The phytoplankton communities of three small boreal forest lakes (L26, L39, and L42) on Ontario's Precambrian Shield (Canada) were investigated over 10 years for possible effects of forest harvesting (logging) within their drainage basins (5 years before logging vs. 5 years after logging). During the postlogging period, higher biovolumes of several taxa were recorded, consistent with previously reported changes in nutrients, chlorophyll, light penetration, and mixing depth. Among the most dramatic changes were increases of 100 and 266% in Cyanophyceae in L39 and L42, respectively, 167% in Dinophyceae in L26, 51 and 130% in Chlorophyceae in L26 and L42, respectively, 182% in Bacillariophyceae in L26, and 53 and 73% in total phytoplankton in L26 and L42, respectively. Other effects associated with logging in the watersheds of these lakes included an increase in the numbers of taxa (in accordance with the intermediate disturbance hypothesis) and a decrease in interannual variability in phytoplankton community structure (in accordance with the ecosystem diversity–stability hypothesis). The less extensive logging of the L26 drainage basin and the maintenance of an unlogged shoreline buffer strip did not preclude apparent effects on phytoplankton comparable with some of those found in the other two lakes, where drainage basin logging was more extensive.

Résumé : Nous avons suivi les communautés phytoplanctoniques de trois petits lacs boréaux (L26, L39 et L42) du Bouclier laurentien en Ontario (Canada) sur une période de 10 ans pour déceler les effets possibles du déboisement (exploitation forestière) de leurs bassins versants (5 années avant le déboisement vs 5 années après le déboisement). Pendant la période qui a suivi le déboisement, nous avons observé des biovolumes accrus chez plusieurs taxons, en accord avec les changements dans les nutriments, la chlorophylle, la pénétration de la lumière et la profondeur de la zone de brassage signalés antérieurement. Parmi les changements les plus spectaculaires, il faut noter les augmentations respectives de 100 % et de 266 % des Cyanophyceae dans les lacs L39 et L42, de 167 % des Dinophyceae du lac L26, de 51 % et de 130 % des Chlorophyceae des lacs L26 et L42, de 182 % des Bacillariophyceae du lac L26 et de 53 % et de 73 % du phytoplancton total des lacs L26 et L42. Comme autres effets du déboisement du bassin versant de ces lacs, on peut signaler l'augmentation du nombre de taxons (en accord avec l'hypothèse de la perturbation intermédiaire) et une diminution de la variabilité de la structure de la communauté phytoplanctonique d'une année à l'autre (en accord avec l'hypothèse de la diversité-stabilité des écosystèmes). Le déboisement moins important du bassin versant et le maintien d'une zone de protection boisée le long de la rive du lac L26 n'ont pas empêché les effets apparents sur le phytoplancton, effets semblables à ceux qui se sont produits dans les deux autres lacs dont le bassin versant a été plus fortement déboisé.

[Traduit par la Rédaction]

Introduction

Most of Ontario's 250 000 lakes are situated in the boreal and Great Lakes – St. Lawrence River forests of the Canadian Shield. Increasing demands for forest products have led to expanding forest management operations, particularly in the boreal forest. Both logging and wildfires have been associated with temporarily increased inputs of dissolved organic carbon, cations, and nutrients to Shield lakes, with effects strongly modulated by lake water renewal time (Bayley et al. 1992; Carignan and Steedman 2000). Short-term studies have shown that the composition and biomass of pelagic and benthic algae in Shield lakes responds to forest disturbance, although impacts may be subtle (Planas et al. 2000; Knapp et al. 2003).

The ecological significance of observed changes in phyto-

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plankton abundance and composition after forest disturbance is difficult to interpret. This is due to a shortage of long-term studies, a rudimentary theoretical context, and the fact that aquatic environment legislation and regulations generally do not specify acceptable variations in water quality and biotic phenomena. Practical protection of aquatic biodiversity in managed forest landscapes requires improved understanding in all three of the above.

In this paper we report on changes in phytoplankton abundance, biodiversity, and community structure in three small, dimictic Precambrian Shield lakes for 5 years before and after experimental watershed and shoreline clearcut logging operations and associated forest regeneration practices. Observed impacts are discussed in terms of existing theoretical perspectives on ecological disturbance and their likely significance to sustainable protection of boreal forest lakes.

Methods

Study area and experimental logging

The study area was part of the Ontario Ministry of Natural Resources' Coldwater Lakes Experimental Watersheds in the boreal – Great Lakes transition forest on the Canadian Shield, approximately 200 km northwest of Thunder Bay, Ontario, Canada (Fig. 1), in the Turtle River – Rainy River drainage basin. The area has shallow soils with abundant boulders and bedrock outcrops, moderate slopes (15–50%), and relief generally not more than about 60 m. Watershed forests consisted of 75- to 100-year-old jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), and black spruce (*Picea mariana*), with some paper birch (*Betula papyrifera*), eastern white cedar (*Thuja occidentalis*), red pine (*Pinus resinosa*), and eastern white pine (*Pinus strobus*).

The study lakes (L26, L39, and L42; none is formally named) are small (surface area 26–39 ha), deep (maximum depth 18–37 m), dimictic, thermally stratified from May through October, and ice covered from November through late April or early May. The lakes have very low concentrations of dissolved substances and are oligotrophic, with Secchi disk visibilities of 7–8 m, specific conductances of about 14–21 $\mu S \cdot cm^{-1}$, dissolved organic carbon concentrations of 2–3 $mg \cdot L^{-1}$, chlorophyll *a* of less than 2 $\mu g \cdot L^{-1}$, and total P of less than 5 $\mu g \cdot L^{-1}$ (Table 1). The lakes contain native populations of lake trout (*Salvelinus namaycush*), white sucker (*Catostomus commersoni*), 5–7 species of smaller fish species (primarily Cyprinidae, Gasterosteidae, Etheostomatinae, and Cottidae), crayfish (*Orconectes virilis*), newts (*Notopthalmus viridescens*), and frogs (*Rana clamitans*). Before the lakes were closed to angling and baitfish trapping in 1992, they were subjected to an intermittent bait fishery and an intermittent, but occasionally intense, lake trout fishery. Zooplankton communities in the lakes are dominated by cyclopoid and calanoid copepods, with total zooplankton densities of approximately 20–60 individuals$\cdot L^{-1}$ (Pinel-Alloul et al., University of Montréal, C.P. 6128, Montréal, PQ H3C 3J7, Canada, unpublished data).

Beginning in 1996 at the midpoint of this 10-year study, the study lakes were subjected to commercial logging and reforestation operations. Most logging occurred over the summer and fall of 1996, but there was some additional logging in 1998. From 1 September to 31 October 1996, L26 had 33% of its watershed area clearcut, with no disturbance of the shoreline forest. The L26 shoreline was left with either an undisturbed shoreline buffer strip 30–90 m wide (with width proportional to shoreline slope), or no cutting at all between the shore and the watershed boundary. In contrast, L39 and L42 had more extensive watershed disturbance (60–70%) in 1996, with 40–60% of the shoreline cleared of all mature jack pine, white spruce, and aspen. Logged shorelines on L39 and L42 retained all riparian shrubs, primarily green alder (*Alnus crispa*), leatherleaf (*Chamaedaphne calyculata*), labrador tea (*Ledum groenlandicum*), and bush honeysuckle (*Diervilla lonicera*), and had no significant soil disturbance. During the 1996 logging, a temporary 30-m shoreline buffer strip was retained along the southwestern shoreline of L42. About 5 km of logging roads were constructed in the combined watersheds of L39 and L42, and about 2 km of roads were constructed in the watershed of L26. Loggers used a tracked feller buncher, chainsaws, and rubber-tired skidders. Trees were dragged by skidders to the nearest road and delimbed there. In July and August 1997, the 1996 clearcuts were scarified by a skidder pulling chains and barrels. Slash piles around the lakes were burned in late October 1997. In June 1998, previously undisturbed subwatersheds draining to L26 (9 ha) and L39 (19 ha) and the L42 temporary buffer strip (~2 ha) were clearcut, increasing total watershed disturbance on L26, L39, and L42 to 45, 77, and 74%, respectively. The 1996 clearcuts were aerially seeded with jack pine at a density of 50 000 seeds$\cdot ha^{-1}$ in 1998. In late August 2000, some upland portions of the 1996 clearcuts were sprayed by helicopter with glyphosate for suppression of aspen, birch, and deciduous shrubs. Sprayed areas included the southern part of the L39 watershed (23 ha), the western part of the L42 watershed (5 ha), and the southwestern part of the L26 watershed (10 ha). The 1998 cuts were not scarified, seeded, or sprayed. Water quality, morphometry, and thermal dynamics of the study lakes are described in more detail in Steedman (2000), Steedman and Kushneriuk (2000), and Steedman et al. (2000).

Phytoplankton sampling and analysis

Phytoplankton samples were collected with a messenger-activated Kemmerer water sampler at a single location (over the deepest point) in each lake at depth intervals of 5 m, starting at a depth of 0.5 m. Individual 500-mL water samples were fixed immediately with Lugol's solution (saturated iodine – potassium iodide + glacial acetic acid) and shipped to the Ministry of the Environment Laboratory in Toronto in 500-mL screw-capped plastic containers. Samples were then concentrated by sedimentation over a 3- to 4-day period in graduated cylinders. Aliquots from each concentrated depth sample for the same collection date were then pooled to produce one integrated sample that represented the water column for that date. The pooled samples were preserved with formaldehyde (~0.7%) and stored in evaporation-proof 25-mL screw-capped vials.

Collections were made throughout the annual period, but to standardize the temporal data and to permit interlake and interannual comparisons, only the pooled samples representing one sampling date per month for the period of May to September of each year were analyzed. In this study, analy-

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Fig. 1. Location of the three lakes (L26, L39, and L42) within the Coldwater Lakes study area, northwest of Lake Superior in Ontario, Canada.

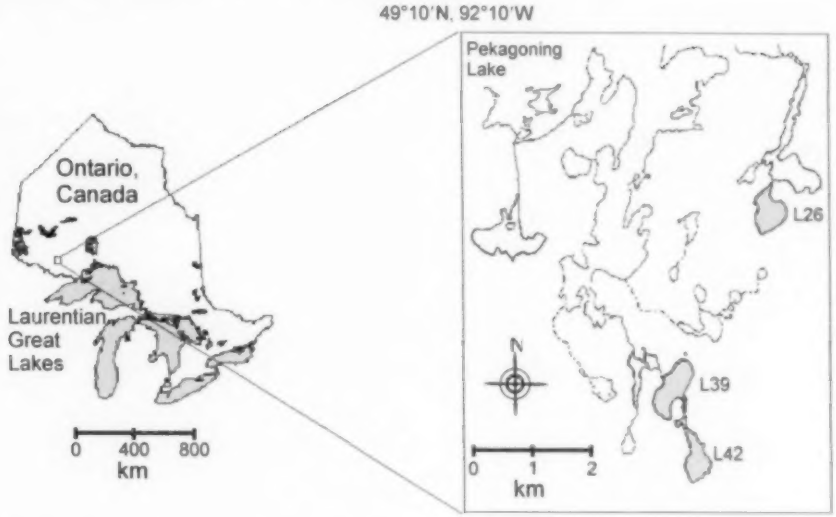

Table 1. Morphometry, habitat, and water quality of study lakes L26, L39, and L42.

	L26	L39	L42
Number of tributary lakes	0	1 (L42)	0
Surface area (ha)	29	39	26
Maximum depth (m)	37	23	18
Lake volume (10^6 m^3)	4.08	4.64	2.15
Total watershed area (ha)	106	194	70
Ratio of terrestrial watershed area to lake surface area	2.6	3.3	1.6
Water renewal time (years)[a]	13.1	8.2	10.5
Littoral habitat area (% lake surface ≤ m depth)	10	8	11
Aquatic vegetation coverage (% littoral area)[b]	2	3	5
September thermocline depth (m)[c]	9.0	9.2	9.4
Secchi depth (m)[c]	8.0	7.0	6.5
Specific conductance ($\mu S \cdot cm^{-1}$)[c]	21.0	16.4	14.4
DOC ($mg \cdot L^{-1}$)[c]	2.2	2.4	2.5
Chlorophyll *a* ($\mu g \cdot L^{-1}$)[c]	0.9	1	1.2
Total phosphorus ($\mu g \cdot L^{-1}$)[c]	3	3	5
Total organic nitrogen ($\mu g \cdot L^{-1}$)[c]	272	230	242
pH[c]	7.1	6.9	6.8

Note: DOC, dissolved organic carbon.
[a]Based on runoff of 0.293 m·year^{-1}, 1995–1997 average (Beaty 1998).
[b]CNFER unpublished data, 1992 (R.J. Steedman, Centre For Northern Forest Ecosystem Research, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada).
[c]1991–2000 average; water quality data are May–September average epilimnetic values.

ses proceeded in a semirandom fashion (interspersed with samples from other locations and not necessarily in chronological order). All phytoplankton identifications and counts reported here were generated by a single person (E.C. Carney) using consistent methods. About 100 samples representing several years of the study were analyzed in 2001. Ten of these had been analyzed at various times over the previous 10 years and served as a test of sample integrity over time (multivariate analyses of total community structure of these duplicates revealed no serious long-term sample storage problems; very high percentages of community similarity values were calculated for the duplicate pairs).

Phytoplankton analysis methods were as described in Nicholls and Carney (1979) using inverted microscopy and Utermöhl-type counting chambers of 2, 5, or 10 mL capacity. Between 300 and 500 "pieces" of algal material (cells, colonies, or portions thereof) were included in the identification and enumeration using 600× magnification; this is considered adequate for acceptable precision (Lund et al. 1958). Improved accuracy for large taxa, for example, *Ceratium* and *Botryococcus*, was achieved by enumerating larger sample aliquots using 150× magnification. Most identifications were taken to the genus level, but some common and unequivocal species were also recorded. Taxa present in the

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sample but too rare to register above the theoretical detection level of 0.5 $mm^3 \cdot m^{-3}$ were assigned a value of 0.25 $mm^3 \cdot m^{-3}$ (where $mm^3 \cdot m^{-3} = \mu g \cdot L^{-1}$, assuming a density of 1 $g \cdot cm^{-3}$ for phytoplankton). All taxa included in the counts were expressed as biovolume by ascribing their morphology to geometric shapes for which volumes could be calculated (spheres, cylinders, cones, etc.) as described in Hopkins and Standke (1992). All biovolume data were measured on cells, not including the intercellular space that exists in some colonial forms.

Data analysis

Data from each sample analyzed (taxonomic name and biovolume) were organized in computer spreadsheet files permitting summation of taxonomic and functional groups. A few May and September months were not represented in the data set (samples not collected). Therefore, for the species richness aspects of the analyses (for which comparable interyear data are essential), the data set was reduced to June, July, and August values.

For some parts of the data analysis, phytoplankton data were grouped into classes to permit comparisons over time and among the three lakes of the numbers of taxa in major taxonomic groups and of the relative abundance of group totals. Some occasionally common species belonging to poorly represented classes were incorporated into "related" and larger classes. One example was *Chrysochromulina*, the only haptophyte genus (Prymnesiophyceae) represented in our samples by at least two species (*C. parva* Lackey and *C. breviturrita* Nicholls); for convenience, it was classified with the Chrysophyceae. Similarly, the synurophycean genera *Mallomonas* and *Synura* were included within the Chrysophyceae. Of the Oscillatoriales, our *Oscillatoria* and *Lyngbya* species may have included some now assigned to the genera *Planktothrix* Anagn. & Komárek, *Limnothrix* Meffert, and *Planktolyngbya* Anagn. & Komárek. We have also retained *Synedra* and *Fragilaria* as separate genera in the Fragilariaceae (sensu Patrick and Reimer (1966)) as opposed to Krammer and Lange-Bertalot's (1991) proposed submersion of *Synedra* within *Fragilaria*. Our taxonomy was based on more traditional conventions and was continued here simply for convenience, not because we necessarily disagree with recent proposals for taxonomic revisions of these groups.

Simple descriptive statistics and nonparametric tests (Mann–Whitney *U* test) were run in CoStat (Cohort Software 1995). Statistical significance was inferred from tables provided in Neave (1981).

For multivariate analyses, taxonomic data were reorganized as follows. (1) Rare taxa were removed; all taxa occurring in fewer than 10% of samples (90 of an initial 182 taxa) were deleted; this step removed 50% of the recorded species, but resulted in only a 2% reduction in total phytoplankton biovolume). (2) All N-fixing cyanophytes (= only *Anabaena* in this case) were grouped. (3) *Oscillatoria* + *Lyngbya* were grouped. (4) All remaining blue-greens were grouped. (5) *Cryptaulax*, *Katablepharis*, and *Pleuromastix* were grouped as "remaining cryptophytes". (6) *Peridiniopsis* + *Peridinium* + *P. inconspicuum* were grouped as "armoured dinoflagellates". (7) A group termed "unidentified chrysophytes" was formed from "unidentified chrysophyte cysts" + "unidentified chrysophyte flagella" + "unidentified chrysomonads". (8) *Kephyrion* and *Pseudokephyrion* were grouped. (9) *Salpingoeca* and *Bicosoeca* were grouped. (10) *Rhizochrysis* and *Chrysidiastrum* were grouped. (11) Eight desmid genera and "unidentified desmids" were grouped under new "total desmids". (12) *Botryococcus* and *Dictyosphaerium* were grouped as the only two members of the family Dictyosphaeriaceae. (13) Five chlorophyte genera were grouped under the family Oocystaceae. (14) Three chlorophyte genera were grouped under "green flagellates". (15) *Coccomyxa* was grouped with "unidentified green". (16) *Cyclotella comta* was grouped with *Cyclotella* spp. All other taxa remained ungrouped, and together with the above 16 groups, comprised a total of 52 "variables" for the multivariate analyses. A complete listing of all taxa (before and after data reduction) is available from the first author upon request.

Calculation and further analysis of phytoplankton community similarities followed Clarke (1993, 1999), utilizing the Bray–Curtis similarity measure on 4th root transformed phytoplankton biovolume data, cluster analysis by a group-averaging algorithm, and ordination by nonmetric multidimensional scaling (NMDS). Each lake-year was designated as a sampling unit (SU), representing a May–October average of all of the phytoplankton variables listed above.

Quantitative assessments of community structure change were made in the context of "within vs. between" site comparisons of community similarity (i.e., are such changes statistically significant?) and utilized the ANOSIM (analysis of similarities) protocol of Clarke and Green (1988; see also Clarke (1999)). Briefly, a test statistic R was computed that reflects the differences in rank similarities between sites contrasted with the differences among sites (or replicates at a site). R ranges from −1 to +1. $R = +1$ only if all replicates within sites are more similar to each other than to any other replicate from any other site. $R = 0$ if H_0 is true (i.e., there is no difference in community structure between sites). The test for significant difference from 0 involved Mantel-type permutation–randomization tests whereby R was calculated a large number of times as the SU labels were randomly reassigned (here 10 000 times or if <10 000, the maximum number of permutations possible given the upper limits imposed by the number of replicates in the groups under comparison). As a result, a frequency distribution of R values was generated to which the original calculated R was compared for probability inference.

The taxa contributing most to significantly different groups of SUs were determined by the SIMPER (similarity percentages) routine in PRIMER (Plymouth routines in multivariate ecological research; Carr 1997) as discussed in Clarke (1993, 1999). Briefly, the contribution of each taxon to the average dissimilarity between all pairs of intergroup SUs (δ) was calculated. Many pairs of samples contribute to $\bar{\delta}_i$, and therefore, if for a particular taxon i, $\bar{\delta}_i$ is large and its standard deviation (SD) is low (i.e., $\bar{\delta}_i/SD(\delta)$ is large), then this taxon is an important, and consistent (because of the low $SD(\delta)$), contributor to the dissimilarity between the groups.

The comparative index of multivariate dispersion (IMD) was calculated according to Clarke and Warwick (1994) from the Bray–Curtis pairwise similarities of all SU pairs (the triangular matrix) to assess the interannual variability in pre- and post-logging treatments. The IMD has a maximum

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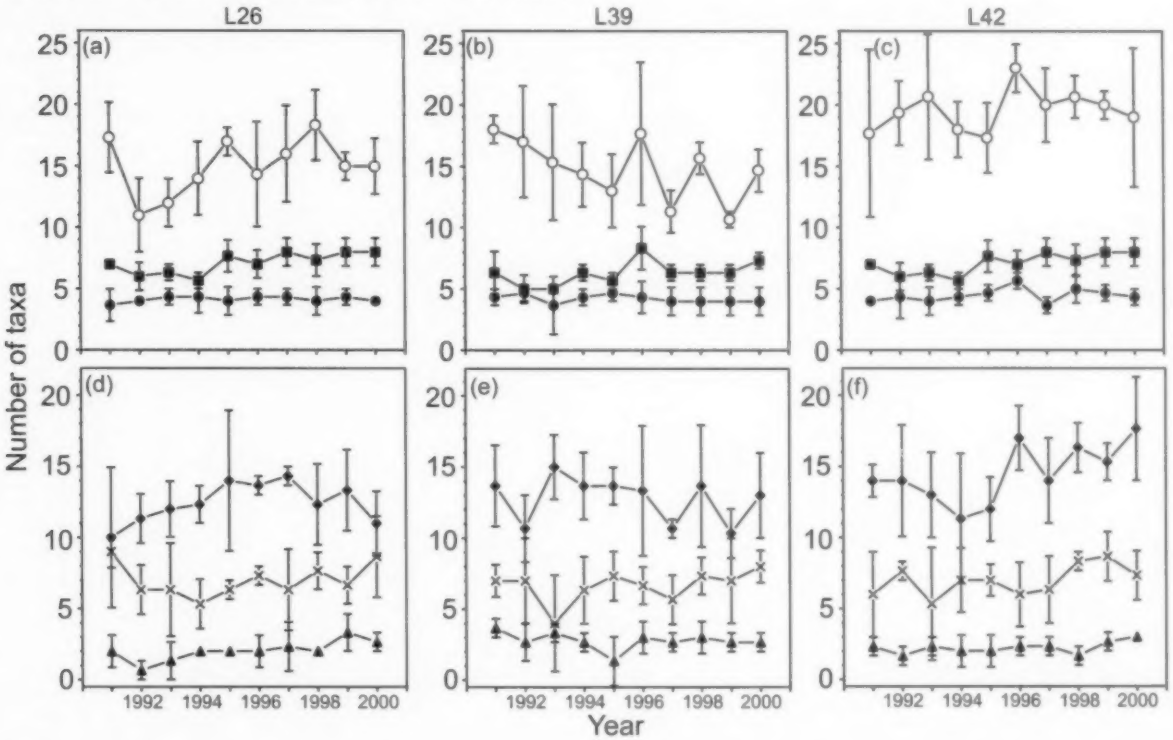
Table 2. Mean numbers of phytoplankton taxa (and related statistics) recorded in samples collected in June, July, and August of each of the five prelogging years (1991–1995) and the four postlogging years (1997–2000) in each of the three lakes (L26, L39, and L42).

	L26		L39		L42	
	Prelogging	Postlogging	Prelogging	Postlogging	Prelogging	Postlogging
Mean	45.1	51.1	48	45.5	50.2	57
SD	5.9	2.9	6.5	6.3	6.3	5.1
CV (%)	13.2	5.9	13.7	14.2	12.8	9.2
Median	45	**51.5***	48	44.5	50	**58***
Maximum	57	55	59	56	60	64
Minimum	34	46	37	34	41	47
Date for maximum	June 1995	Aug. 1997	Aug. 1993	Aug. 1998	Aug. 1991 July 1992 Aug. 1993	June 2000
Date for minimum	June 1992	June 1997	June 1993	June 1999	June 1993	Aug. 2000

Note: The dates of the samples harboring the maximum and minimum numbers of taxa are also given. Significantly increased medians ($P < 0.05$; Mann–Whitney U tests) are indicated in bold and with an asterisk (*). SD, standard deviation; CV, coefficient of variation.

Fig. 2. June, July, and August mean numbers of taxa (±95% confidence intervals) for each of the dominant classes of phytoplankton in each of the lakes (L26, L39, and L42) from 1991 to 2000: ○, Chlorophyceae; ■, Bacillariophyceae; ●, Cryptophyceae; ×, Cyanophyceae (Cyanobacteria); ▲, Dinophyceae; ◆, Chrysophyceae.



value of +1 when all pairwise similarities among "impacted" SUs (here, postlogging) are lower than any similarity value for paired SUs representing the "control" (prelogging) set; the converse is true when IMD = –1. IMD values near zero imply no difference in the variability between groups.

Throughout the multivariate approaches described above, the years within each of the pre- and post-logging treatment time periods (1991–1995 vs. 1997–2000) at each of the lakes were all treated as within-treatment replicates. Individual SUs within treatments were evaluated only in the context of the significance of "between vs. within" treatment differences (except for outlying SUs for which it was instructive to determine which taxa contributed most to its outlier status — the SIMPER routine in the PRIMER program).

Results

Numbers of taxa

Based on the June, July, and August samples, the median numbers of taxa in L26, L39, and L42 ranged from 45 to 58

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Table 3. Median and mean (with related statistics) biovolumes of dominant phytoplankton classes (and total phytoplankton) during the May–September periods of the prelogging (1991–1995) and postlogging years (1997–2000) in L26, L39, and L42.

		L26		L39		L42	
		Prelogging	Postlogging	Prelogging	Postlogging	Prelogging	Postlogging
Cyanophyceae	Mean	13.7	13.3	6	13	10.2	20
	SD	15	13.5	6.7	11.1	9.8	19
	CV (%)	110	102.6	111.7	86.4	96.8	96.2
	Median	9.5	6	3.5	**7.0***	4.5	**16.5***
Dinophyceae	Mean	6.8	13.9	12.8	11.2	8.9	13.3
	SD	6	12.9	11.6	9.2	6.4	11.8
	CV (%)	88.7	93.7	91.6	83.2	72.6	90.2
	Median	3	**8.0***	12	8	8	8
Cryptophyceae	Mean	19.3	19.4	25.6	26.5	57.1	41.6
	SD	17.7	13.6	23.8	17.4	46.6	34.1
	CV (%)	92.7	71.2	94.1	66.4	82.5	83
	Median	13.2	18	11	20	34.3	38.5
Chrysophyceae	Mean	57.3	60.9	95.3	118.2	172	107
	SD	27.8	28.3	86.5	62.7	327	78.2
	CV (%)	49.1	47	91.7	53.7	192	74.2
	Median	50.3	60.3	65.8	83.3	70	74.3
Chlorophyceae	Mean	18.2	23.7	42.7	185.8	48	52.4
	SD	9.1	7.7	33.6	202.1	28.8	35.5
	CV (%)	50.3	32.9	79.4	110.2	60.5	68.5
	Median	13.8	**20.8***	39.3	**90.5***	36.3	39
Bacillariophyceae	Mean	101	153.7	87.3	106	58.5	69.9
	SD	66.1	64.1	55.9	57.9	34.2	80.8
	CV (%)	65.9	42.3	64.7	55.3	59.1	117
	Median	56.3	**158.8***	63	80	40.3	42.3
Total phytoplankton	Mean	217	285.3	269.6	460.9	356	305
	SD	72.6	75.4	135.5	246.3	362	183
	CV (%)	33.8	26.8	50.8	54.1	103	60.6
	Median	181	**277.3***	226.8	**392.0***	188	222

Note: Significant changes in medians ($P < 0.05$; Mann–Whitney U tests) are indicated in bold with asterisks (*). SD, standard deviation; CV, coefficient of variation.

(Table 2). In L26 and L42, the numbers of taxa increased after logging. Maximum and minimum numbers of taxa occurred predominantly in August and June, respectively (Table 2).

Chlorophytes contributed most to the total numbers of taxa in all three lakes with 10-year mean numbers of 15.0, 14.8, and 19.6 in L26, L39, and L42, respectively. Next most important were the Chrysophyceae with averages of 12.4, 12.8, and 14.5 taxa per year in L26, L39, and L42, respectively, followed by the Cyanophyceae with 7.0, 6.6, and 7.0 taxa and the Bacillariophyceae with 10-year means of 7.1, 6.3, and 5.9 taxa in L26, L39, and L42, respectively (Fig. 2). Far fewer taxa represented the Cryptophyceae (4.1, 4.2, and 4.5), the Dinophyceae (2.0, 2.8, and 2.2), and the Euglenophyceae (0.2, 0.1, and 0.3) in L26, L39, and L42, respectively.

Some patterns were apparent in the temporal distribution of the numbers of taxa in some of these classes. For example, taxon numbers in the Dinophyceae and Chlorophyceae in L39 declined during the prelogging period (Figs. 2*b*, 2*e*), whereas those in the Cyanophyceae in L26 declined during the prelogging and increased during the postlogging periods (Fig. 2*d*), the Chrysophyceae at this location reflected a mirror image of the cyanophyte pattern, increasing numbers before logging and then declining after logging (Fig. 2*d*). Numbers of Chrysophyceae in L42 (Fig. 2*f*) and Bacillariophyceae in L26 and L39 (Figs. 2*a*, 2*b*) were higher during the postlogging period. Minimum numbers of Dinophyceae and Chlorophyceae in L26, Chrysophyceae and Bacillariophyceae in L39, and Dinophyceae in L42 all occurred in 1992.

Biovolume changes

Total phytoplankton biovolumes in the three lakes were very similar, with May–September means ranging between 217 and 461 $mm^3 \cdot m^{-3}$ (Table 3). In L26, peak biovolume of 414 $mm^3 \cdot m^{-3}$ occurred in June of 1996; major contributors were the chrysophytes *Chromulina* (42 $mm^3 \cdot m^{-3}$), *Synura* (38 $mm^3 \cdot m^{-3}$), chrysophyte stomatocysts (33 $mm^3 \cdot m^{-3}$), and *Mallomonas* (17 $mm^3 \cdot m^{-3}$). Chlorophyceae were also well represented at this time, with contributions by *Botryococcus* (18 $mm^3 \cdot m^{-3}$), *Oocystis* (7 $mm^3 \cdot m^{-3}$), and *Gloeocystis* (5 $mm^3 \cdot m^{-3}$). The Cyanophyceae were relatively important in 1991 and 1999 when *Anabaena*, *Aphanothece*, and *Chroococcus* dominated the class. Dinoflagellates were highest in 2000, with May and September biovolumes of 54 and 27 $mm^3 \cdot m^{-3}$, respectively; the most important genera were *Gymnodinium*, *Peridinium*, and *Ceratium*.

In L39, peak phytoplankton biovolumes occurred in June (1104 $mm^3 \cdot m^{-3}$) and September (1028 $mm^3 \cdot m^{-3}$) of 1999. About 60% of these peaks were contributed by the chloro-

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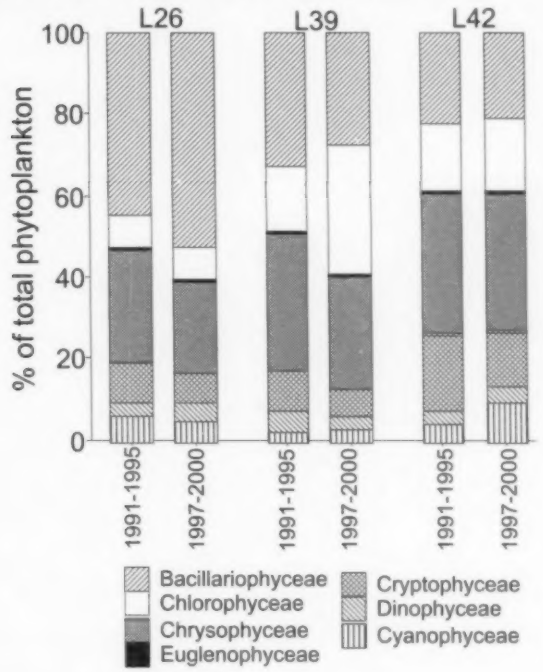

Fig. 3. Average phytoplankton class contributions (%) to total phytoplankton during prelogging (1991–1995) and postlogging (1997–2000) time periods in lakes L26, L39, and L42.

phyte *Botryococcus*. Two lesser peaks in 1993 (506 $mm^3 \cdot m^{-3}$) and 1994 (676 $mm^3 \cdot m^{-3}$) were contributed by Chrysophyceae totals of 335 and 352 $mm^3 \cdot m^{-3}$, respectively, represented by several chrysophyte genera, including *Chromulina*, *Dinobryon*, *Chrysidiastrum*, unidentified chrysomonads, and chrysophyte stomatocysts. Maximal dinoflagellate biovolume occurred in 1991 in L39.

In L42, a spring bloom of the chrysophyte *Uroglena* with biovolumes of 956 and 1223 $mm^3 \cdot m^{-3}$ on 30 May and 13 June 1995 (92 and 85%, respectively, of total Chrysophyceae biovolume) helped elevate the total phytoplankton biovolumes to 1438 and 1595 $mm^3 \cdot m^{-3}$, respectively, the highest recorded in the study. Other smaller peaks in total biovolume in the range of 500–750 $mm^3 \cdot m^{-3}$ occurred in 1994, 1996, 1997, and 2000. The Chrysophyceae, Bacillariophyceae, and Chlorophyceae were the main constituents of these peaks; the Cyanophyceae and Dinophyceae were also consistent but less important contributors.

Diatoms (Bacillariophyceae) were a much more important portion of the total phytoplankton in L26 than in L39 or L42, but at the expense of the green algae (Chlorophyceae), Chrysophyceae, and Cryptophyceae, which contributed only about 35% of the total in L26 but nearly 70% in L42 (Fig. 3). There were clear tendencies to increases in phytoplankton class biovolumes after the initiation of logging in the drainage basins of all three lakes. Of the seven groups for which statistical summaries were computed (including total phytoplankton, but omitting the Euglenophyceae because of consistently undetectable biovolumes), there were 21 potential changes resulting from the pre- vs. post-logging comparisons (7 groups × 3 lakes). The median values representing each of these lake–phytoplankton groups increased after logging in 18 instances, decreased only twice, and was unchanged in one case (Table 3). Among the most dramatic changes were increases of 100 and 266% in Cyanophyceae in L39 and L42, 167% in Dinophyceae in L26, 51 and 130% in Chlorophyceae in L26 and L42, 182% in Bacillariophyceae in L26, and 53 and 73% in total phytoplankton in L26 and L42 (Table 3).

In each of the three lakes, approximately 50% (range = 37–58%) of the average pre- and post-logging phytoplankton biovolume was contributed by just five taxa, and only 11 different taxa in total were ranked among the dominant five during each treatment of the three lakes. With respect to dominant taxa, L26 was the least changed following logging; the same five taxa dominating the prelogging phytoplankton community were also the highest ranked during the postlogging period, although the order of importance was changed slightly (Table 4).

Whole community (multivariate) change

Multivariate analysis of all three lakes together revealed some clear patterns in phytoplankton community associations; the intralake associations appeared to be stronger than interannual groupings related to pre-and post-logging periods because some strong pre- and post-logging phytoplankton associations were not found consistently among all three lakes. For example, cluster *i* (Fig. 4) consisted of seven L42 SUs that included both pre- and post-logging years. The two most similar pair of SUs (90% Bray–Curtis similarity level) were the 1999 and 2000 phytoplankton communities in L26 (part of cluster *ii*, Fig. 4). Similarly, other postlogging phytoplankton communities with relatively high similarities included those occurring in 1998, 1999, and 2000 in L39 (cluster *v* in Figs. 4, 5*b*). Other strong phytoplankton associations included those representing some of the prelogging years (e.g., the 1993–1994 and the 1991–1992 communities in L39 (clusters *iii* and *iv*, respectively, in Fig. 4)). The 1991 and 1992 communities of L26 (pair *vi* in Fig. 4) had a relatively low level of similarity with all other SUs and when grouped with other prelogging SUs from this lake suggested a high degree of interannual variability (widely separated in the ordination plane in Fig. 5*a*). The 1995 SU from this subset intrudes on an otherwise very well-defined postlogging group of SUs from L26 (broken-line enclosure in Fig. 5*a*) for which interannual variability was very low. The prelogging SUs for L39 also showed a high degree of interannual variability in both the cluster analysis and the ordination. With the exception of 1998 in L42, which had a phytoplankton community most resembling the one found in 1991 in L42, the postlogging years 1996–2000 all had relatively similar phytoplankton communities in L42 (Fig. 5*c*).

The ANOSIM analyses (Table 5) detected logging effects in L39 only, where 1991–1997 phytoplankton communities were found to differ significantly from those of 1998–2000 ($P = 0.017$). Both the ordination and the clustering analyses suggested that year-to-year variability was greater before the onset of logging operations. This was tested formally with measurements of the IMD. Although no statistical inferences can be applied to the results of this test, it is important to note that of the six comparisons made (three lakes, each with two different pre- vs. post-logging time scenarios), all

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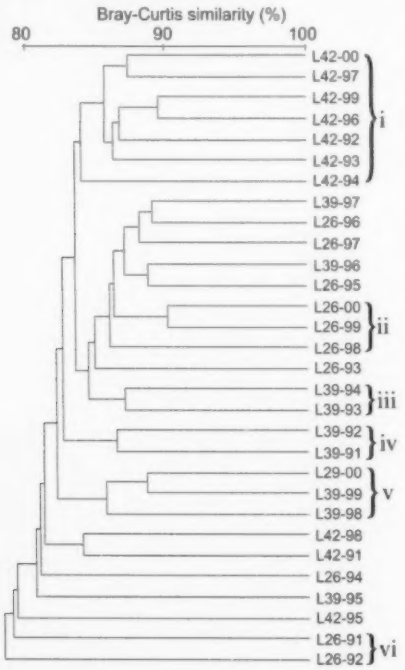
Table 4. The five most dominant taxa (% of total biovolume) during prelogging (1991–1995) and postlogging (1997–2000) time periods in each of the three lakes (L26, L39, and L42).

Prelogging period		Postlogging period	
Taxa	% of total biovolume	Taxa	% of total biovolume
L26			
Rhizosolenia	13.4	*Cyclotella comta*	17.9
Cyclotella comta	12.1	*Rhizosolenia*	17.6
Asterionella	9.9	*Cyclotella*	7.4
Cryptomonas	8.7	*Asterionella*	6.6
Cyclotella	5.1	*Cryptomonas*	5.2
Total, %	49	Total, %	55
L39			
Unidentified chrysophyte cysts	9.3	*Botryococcus*	28.8
Botryococcus	9.1	*Asterionella*	8.8
Cyclotella comta	7.6	*Rhizosolenia*	5.5
Unidentified chrysomonads	7.4	*Cryptomonas*	5.5
Cyclotella	7.2	*Chromulina*	5.4
Total, %	41	Total, %	54
L42			
Synura	25.8	*Cryptomonas*	10.9
Cryptomonas	14.2	*Tabellaria*	7
Unidentified chrysomonads	6.9	*Rhizosolenia*	6.7
Tabellaria	6.4	*Botryococcus*	6.5
Chromulina	4.2	Unidentified chrysophyte cysts	5.9
Total, %	58	Total, %	37

Fig. 4. Cluster analysis dendrogram of phytoplankton communities in the three lakes over the 1991–2000 period of investigation. L42-00 represents the 2000 sampling unit for L42; L39-97 represents the 1997 sampling unit for L39, etc.



of them showed higher relative measures of dispersion for their prelogging treatment periods than for the postlogging periods; however, for one of these (L42, second time scenario), the difference was very small (Table 6). Of the three lakes, L26 showed the greatest difference in pre- vs. postlogging interannual phytoplankton community variability (Table 6), despite the continued domination by the same five taxa contributing 49 and 55% of the total phytoplankton biovolume during the pre- and post-logging periods, respectively (Table 4).

Discussion

Exclusion of the May and September samples resulted in only minor decreases in the total numbers of recorded taxa over those for the June–August periods; however, by restricting the period to June–August (owing to a few missing sample results for May and September), we have ensured that the same numbers of samples were compared among the Coldwater Lakes data set over all 10 years of the study, thus precluding sample number effects on species richness determinations, which can be significant, according to Arnott et al. (1998) and Hubálek (2000). The numbers of phytoplankton taxa observed in the three lakes (generally averaging 45–60) are considerably higher than those reported for strongly acid-stressed lakes of the Sudbury region in south-central Ontario but are in agreement with the numbers reported for less acidic lakes in the same region having alkalinities in the 2–10 mg $CaCO_3 \cdot L^{-1}$ range (Nicholls et al. 1992). Mean prelogging alkalinity values for L26, L39, and L42 were 8.3, 5.9, and 4.9 mg $CaCO_3 \cdot L^{-1}$, and postlogging changes in specific conductance, alkalinity, pH, and total phosphorus and sulphate were undetectable in these lakes (Steedman 2000), so increased numbers of taxa re-

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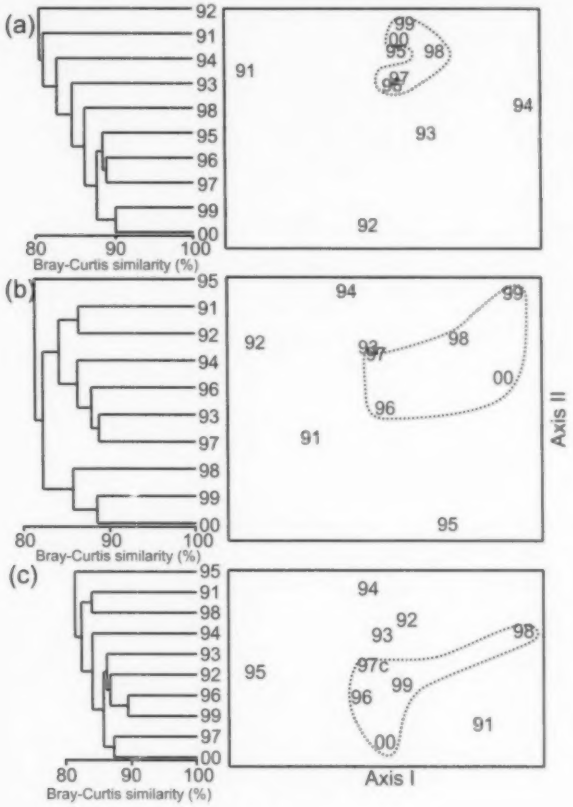
Fig. 5. Dendrograms and nonmetric multidimensional scaling (NMDS) ordinations of phytoplankton communities in the three lakes ((*a*) L26, (*b*) L39, and (*c*) L42) for the years 1991 to 2000.



corded during the postlogging time period may not have been related to changes in fundamental water chemistry.

The relative contributions of the phytoplankton classes to the total numbers of taxa in the Coldwater Lakes were similar to those found for Sudbury area lakes, except that the Dinophyceae were less important than the Cryptophyceae in the Coldwater Lakes; this is consistent with other observations from Sweden and Ontario linking the importance of dinoflagellates to high acidity (Nicholls et al. 1992; Findlay and Kasian 1996; Hörnström 1999).

The shift towards greater diversity (higher taxon numbers) in L26 and L42 following initiation of logging operations may reflect the imposition of some environmental stress associated with logging on the watersheds of these lakes. Other changes in the phytoplankton included (*i*) increased biovolume of several taxa, which is consistent with increased chlorophyll *a* in these lakes (Steedman 2000; Knapp et al. 2003) and with algal increases observed in other lakes after logging (Planas et al. 2000; Prepas et al. 2001), and (*ii*) decreased interannual variablility in phytoplankton community structure. It is useful to evaluate these changes in the context of ecosystem theory, specifically, the Intermediate Disturbance Hypothesis (IDH) and the diversity–stability hypothesis.

We have used taxon richness as our measure of phytoplankton diversity. Hubálek (2000) evaluated 24 measures of

Table 5. Results of analyses of phytoplankton community structural differences before and after logging (one-way ANOSIM (analysis of similarities)).

	1991–1995 vs. 1996–2000		1991–1997 vs. 1998–2000	
Lake	Global *R*	Probability (%)	Global *R*	Probability (%)
L26	0.1	10.3	–0.131	68.3
L39	0.232	8.7	0.536	1.7
L42	0.076	23	0.06	35

Note: Two different temporal scenarios were used to define the pre- and post-logging periods: (1) 1991–1995 vs. 1996–2000 and (2) 1991–1997 vs. 1998–2000. The second scenario assumes that the effects of initial logging in 1996 were delayed for 2 years to coincide with renewed logging operations that began again in 1998.

species diversity with reference to 20 criteria (intuitively desirable features of a good diversity measure) and concluded that species richness (simple numbers of species) was one of the four best, provided that sample sizes were approximately equal. Most taxa in our lists were recorded as genera, and the level of taxonomic analysis applied to the Coldwater Lakes samples was kept constant over the years of the study (and by the same analyst (E.C. Carney)), so that ecological concepts applied to species richness should also apply to our genus richness data. Maintenance of diversity depends on highly complex and interacting mechanisms that foster species co-existence (Chesson 2000). As well, species richness can change substantially in response to environmental change. It is an emergent consequence of ecosystem processes and can be maintained within narrow limits only if system productivity and resource availability are kept within narrow limits and if opportunities exist for continued loss and gain of species from an extrinsic pool (Brown et al. 2001). When an environmental stress is applied to a boreal forest lake, a reasonable expectation is that phytoplankton diversity might change. When that stress is removed, species diversity should revert to its previous prestressed state at a rate dependent on the intrinsic resilience of the system and on the availability (proximity) of species in nearby similar, but unstressed, lakes, so that inoculation of suitable species can occur relatively soon after the disturbance is removed (mediated by avian, hydrologic, and atmospheric transfer mechanisms). The magnitude of diversity change in response to environmental stress is theoretically related to the magnitude of the stress applied (its severity, duration, and frequency).

The IDH was proposed by Connell (1978) to explain the high biodiversity of tropical rain forests and coral reefs. A parallel phenomenon in pelagic systems was termed the "paradox of the plankton" by Hutchinson (1961) in describing the high numbers of species co-existing in lake plankton communities. Briefly, the IDH has the following tenets: (*i*) biotic diversity will be low in a community experiencing constant low levels of stress or disturbance because of competitive exclusion; (*ii*) diversity will also be low in communities subjected to a high level of disturbance because only a few very opportunistic and invasive species can cope with constant and excessive disturbance of their habitat; and (*iii*) highest levels of diversity should be found in communities experiencing moderate stress as a consequence of constant "jockeying" for ecological niche; a changing environment favours larger numbers of species having environmental

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Table 6. Results of index of multivariate dispersion (IMD) tests comparing the relative interannual variability among pre- and post-logging phytoplankton communities.

	1991–1995 vs. 1996–2000		1991–1997 vs. 1998–2000	
Lake	Relative dispersion	IMD value	Relative dispersion	IMD value
L26	1.48 vs. 0.52	1	1.08 vs. 0.43	0.68
L39	1.12 vs. 0.88	0.26	1.06 vs. 0.61	0.46
L42	1.21 vs. 0.79	0.44	1.01 vs. 0.93	0.08

Note: The two values given for relative dispersion represent the two time periods under comparison. Two different temporal scenarios were used to define the pre- and post-logging periods: (1) 1991–1995 vs. 1996–2000 and (2) 1991–1997 vs. 1998–2000. The second scenario assumes that the effects of initial logging in 1996 were delayed for 2 years to coincide with renewed logging operations that began again in 1998.

tolerances within the ranges created by the disturbance, but where environmental optima are not likely to exist for any (or few) species.

The IDH was explored for its applicability to phytoplankton (Padisák et al. (1993) and references therein). More recent experimental and empirical data lend support for this theory for phytoplankton response to environmental stress (Polishchuk 1999). The response of the Coldwater Lakes phytoplankton to logging appears to be another example of increased diversity resulting from environmental stress. That the disturbance associated with the logging operations in the watersheds of these lakes was at an "intermediate" level is debatable, but other limnological evidence strongly suggests that it was. Summer average water clarity in these lakes declined by 25%, and thermocline depths decreased by about 10% after logging, but because neither was statistically significant (Steedman and Kushneriuk 2000), it is certainly unrealistic to classify these as severe disturbances. Similarly, Steedman (2000) reported increases of 10–40% in concentrations of dissolved organic carbon, chlorophyll, total nitrogen, potassium, chloride, and silicate, along with declines in calcium and magnesium of 10–25%. The limiting factor for planktonic primary producers in boreal forest lakes is usually phosphorus availability (Schindler et al. 1978). Interestingly, no statistically significant changes in phosphorus concentrations in any of the three lakes were detected following logging (Steedman 2000), yet phytoplankton biomass increased, perhaps in response to very low increases in phosphorus loading from the drainage basins, together with the more significant measured increases in silicon and nitrogen (Steedman 2000).

Competition for nutrients in lake phytoplankton is a mechanism whereby community structure is continually changing (Interlandi and Kilham 2001). Higher levels of nutrients in the Coldwater Lakes following logging, along with the change in mixing zone depth ("...in stratifying lakes, increases in the mixing depth would be an ideal indicator of physical disturbance..." (Sommer et al. 1993)), are likely related to the changes in phytoplankton community structure (higher numbers of taxa, higher biovolume).

In the Coldwater Lakes, increased phytoplankton diversity was associated with a decrease in interannual variability in community structure (decreases in IMD), thus lending support to the diversity–stability theory. That ecosystem diversity begets ecosystem stability is an important ecological precept that was convincingly demonstrated by McNaughton (1993) and Tilman and Downing (1994) for grassland ecosystems, where species richness was determined solely by interspecies competition for the single trophic level under investigation. Aoki and Mizushima (2001) have apparently demonstrated for the first time the applicability of the diversity–stability hypothesis for more complex aquatic ecosystems with multiple trophic levels.

This study of phytoplankton change over time could not include true controls on logging effects, because lakes with morphometric, physical, chemical, and biological characteristics identical to those of our study lakes undoubtedly do not exist. Interannual climate variability may have influenced the long-term trends in phytoplankton in the Coldwater Lakes, and inferences about logging effects on our three lakes, especially those aspects relating to interannual variablility in phytoplankton composition, are perhaps somewhat speculative. Heyen et al. (1998) showed that climate variability can be an important cause of interannual variability in marine zooplankton. The coolest summer of the past several decades for eastern North America (and indeed over much of the earth) was in 1992, caused by the 1991 eruption of Mount Pinatubo in the Philippines (Kerr 1993). Numbers of phytoplankton taxa for several groups were the lowest recorded in 1992. Dinophyceae and Chlorophyceae in L26, Chrysophyceae and Bacillariophyceae in L39, and Dinophyceae in L42 all achieved their lowest numbers of taxa in 1992.

Although interannual variations in climate most certainly contributed to the variability in phytoplankton community structure in the Coldwater Lakes study area, it was beyond the scope of this paper to explore this in detail. As data collection continues and longer postlogging time series are accumulated, testing specifically for climate effects will become a primary focus of future analysis of the Coldwater Lakes data, especially as statistical methods for answering these kinds of questions are being refined (Heyen et al. 1998). Certainly, climate change has the potential to override many other anthropogenic perturbations in aquatic environments (Freedman and Beauchamp 1998; Schindler 2001) and has demonstrated significance for lake phytoplankton of the boreal forest region (Arnott et al. 2001; Findlay et al. 2001). At this time, our data do demonstrate, however, that apparent logging effects on phytoplankton were of about the same degree of severity as those reported previously for other limnological variables in these lakes and were also consistent with the interlake differences in limnological effects. In particular, the less extensive logging of the L26 drainage basin and the maintenance of an unlogged buffer strip along the L26

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shoreline did not preclude apparent effects on phytoplankton as great as those found in the other two lakes with more extensive logging of their drainage basins.

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Modeling time-varying growth using a generalized von Bertalanffy model with application to bloater (*Coregonus hoyi*) growth dynamics in Lake Michigan

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Abstract: A concurrent increase in lakewide abundance and decrease in size-at-age of bloater (*Coregonus hoyi*) in Lake Michigan have suggested density-dependent growth regulation. We investigated these temporal patterns by fitting a dynamic von Bertalanffy model and length–weight relationship with time-varying parameters to mean length- and weight-at-ages (ages 1–7) from annual surveys (1965–1999). We modeled yearling length, asymptotic size (L_∞), and the parameters of a power relationship between mean weight and mean length (α and β) as changing slowly over time using a random walk model. The Brody growth coefficient (k) was modeled as a linear function of L_∞ with year-specific random deviations. Our results support a positive relationship between L_∞ and k, indicating that under conditions supporting larger asymptotic lengths, individuals approach the asymptote more rapidly. We explored the relationship between year-specific growth parameters and indices of lakewide bloater abundance and found evidence of density-dependent growth. However, in the most recent years, L_∞ and yearling length have remained low in Lake Michigan despite low bloater abundances, suggesting the occurrence of a fundamental shift in the food web.

Résumé : Chez le cisco de fumage (*Coregonus hoyi*) du lac Michigan, la coïncidence d'une augmentation de l'abondance dans tout le lac et d'une diminution de la taille à un âge donné laisse croire à l'existence d'une régulation de la croissance dépendante de la densité. Nous avons examiné ces structures temporelles en ajustant un modèle dynamique de von Bertalanffy et des relations longueur–masse avec des paramètres qui varient dans le temps aux données de longueur moyenne et de masse à un âge donné (âges 1–7) provenant d'inventaires annuels (1965–1999). Nous avons modélisé la longueur des jeunes de 1 an, la longueur à l'asymptote (L_∞) et les paramètres d'une relation de puissance entre la masse moyenne et la longueur moyenne (α et β) en les faisant varier lentement dans le temps à l'aide d'un modèle de marche aléatoire. Le coefficient de croissance de Brody (k) a été modélisé comme une fonction linéaire de L_∞ avec des déviations aléatoires spécifiques à l'année. Nos résultats indiquent une relation positive entre L_∞ et k, ce qui veut dire que, dans des conditions qui permettent des longueurs à l'asymptote plus élevées, les individus s'approchent plus rapidement de l'asymptote. Nous avons étudié la relation entre les paramètres de croissance spécifiques à l'année et les indices d'abondance des ciscos dans l'ensemble du lac et nous avons trouvé des indications d'une croissance dépendante de la densité. Cependant, durant les dernières années, L_∞ et la longueur des jeunes de 1 an ont été faibles au lac Michigan malgré l'abondance réduite de ciscos, ce qui laisse croire à un changement radical dans le réseau alimentaire.

[Traduit par la Rédaction]

Introduction

Dynamic growth of fishes has many implications and applications in the management of fisheries, and many ecological and practical insights can be gained by examining patterns in fish growth (e.g., Ferreri and Taylor 1996; Fargo and Kronlund 2000; Walters and Wilderbuer 2000). The effects of environmental factors on growth have been examined through both experimental manipulation and observational studies. Although the experimental approach allows the strongest inferences, it is often not feasible for populations or species of interest. In many cases when an observational approach is necessary, a time series of observations of size-at-age and environmental factors are examined (e.g., Mallet et al. 1999; Millar et al. 1999; Fargo and Kronlund 2000). Because of the high variability in mean size-at-age estimates about the population's true

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mean size-at-age, it is often advantageous to identify and fit a growth model to the data to provide smoothed estimates of growth over time.

Such a model-based analysis of data from an observational study generally extends a traditional growth model, usually the von Bertalanffy model, to include time-varying parameters fit to the time series of observations (e.g., Mallet et al. 1999; Millar et al. 1999; Fargo and Kronlund 2000). The time series of observations used to fit the model is generally one of two types, size-at-age data or growth increment data calculated from size-at-age data.

Time-varying parameters have been incorporated into growth models in two general ways, through explicit functions of an environmental variable or by estimating, independently of environmental data, year-specific parameters for the growth model. Applications of the first approach (Millar and Myers 1990; Mallet et al. 1999; Millar et al. 1999) usually model either the L_∞ or k parameter of a von Bertalanffy growth curve as function of an environmental factor, usually temperature. This approach requires identifying both the environmental factor and the functional relationship between this factor and the growth parameters. If the connection between growth and the environment is misspecified, it is possible that spurious patterns in year-specific growth could be identified.

The second approach is to fit a growth model to data on size-at-age independently for each year for which data are available (e.g., Zhao et al. 1997; Fargo and Kronlund 2000). The temporal patterns in the resulting parameter estimates can then be examined in relation to temporal patterns in factors that might cause them to vary. By independently fitting a growth model to each year of size-at-age data, however, this approach ignores the interdependence of growth between years. Here, the model is describing the pattern in size-at-age within a year, not mean growth of a given age between year y and year $y + 1$. The two are only equivalent when growth rates are not changing over time. Hence, this approach causes difficulties in interpretation.

Here we present an alternative method for applying the second approach. We use a von Bertalanffy growth curve with time-varying parameters to predict growth increments from one year to the next. We keep track of the dynamically changing predictions of size-at-age and compare these predictions with a time series of size-at-age observations to estimate the parameters of our model. Thus, the time-varying parameters are estimated independently of any proposed environmental mechanism, in contrast with the first method, and the parameters describe growth rather than year-specific patterns in size-at-age, as in many applications of the second method. Our technique uses a time series approach to model the changes in growth parameters over time and estimates these parameters using a maximum likelihood framework. We apply this approach to the growth dynamics of the bloater (*Coregonus hoyi*) population in Lake Michigan. We then explore the potential mechanisms for changes in bloater growth using the resulting growth parameter estimates.

Bloater is an important member of the Lake Michigan ecosystem. In Lake Michigan, this coregonine is the sole remaining member of an original endemic complex of deepwater forms (Todd et al. 1981). Historically, bloater populations supported valuable commercial fisheries (Brown et al. 1987; Fleischer 1992) and were forage for the native lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*) populations. Currently, they are forage for the array of stocked salmonids, especially when bloater are younger and smaller (Holey et al. 1998; Madenjian et al. 2002). Changes in bloater populations within Lake Michigan have been dramatic. Bloater abundance increased from near zero in 1970 to dominate the planktivore biomass of the lake by the late 1980s (Madenjian et al. 2002) (Fig. 1*a*). Bloater abundance remained high during most of the 1990s and subsequently declined to low levels again (TeWinkel et al. 2002). Concurrent with these large changes in abundance, bloater length- and weight-at-age also went through large changes (Figs. 1*b*–1*d*). These changes in size-at-age appeared to be correlated with bloater abundance, suggesting that bloaters in Lake Michigan might be exhibiting density-dependent growth (TeWinkel et al. 2002). Because bloater length- and weight-at-age have been monitored continuously since 1965 to present (except 1966 and 1998), these data provided us the opportunity to explore the changes that have occurred in the growth of bloater over time and the potential for density-dependent growth regulation in the Lake Michigan bloater population.

Materials and methods

The Lake Michigan bloater population has been assessed annually since 1962 by the U.S. Geological Survey (USGS) – Great Lake Science Center in a fall bottom trawl survey. This survey is conducted at fixed locations throughout Lake Michigan and provides information on the size (length and weight), age composition, and abundance (through catch-per-unit-effort (CPUE)) of the bloater population along with the exotic alewife (*Alosa pseudoharengus*) population. We used these survey data to construct a time-varying growth model for the bloater population and explored the relationship between the estimated growth parameters and abundance of both bloater and alewife.

Fall trawl survey design

To calculate mean length- and weight-at-age and abundance indices, we analyzed catch data from annual bottom trawl surveys conducted by the USGS – Great Lakes Science Center each fall (e.g., Hatch et al. 1981). The survey was initiated in 1962, but bloater were first aged in 1965 and hence we restricted our analysis to the 1965–1999 period. Trawls were generally 10 min in length and used a ¾ Yankee Standard No. 35 bottom trawl (12 m headrope, 15.5 m footrope, and 13-mm mesh in the cod end) dragged on contour during the day as described by Hatch et al. (1981). Sampling was done offshore of fixed shore locations (Fig. 2). Generally tows were made at each location at 9-m depth intervals and the sampled depths ranged from 6 to 128 m. Not all locations were sampled in each year, usually related to weather conditions, nor were all depths sampled at each location because of irregular bottom features. Although the locations were fixed, the number and identity of sampled locations did change over time. Initially, from 1962 to 1966, trawls were made only off Saugatuck, Mich. (Fig. 2), and in

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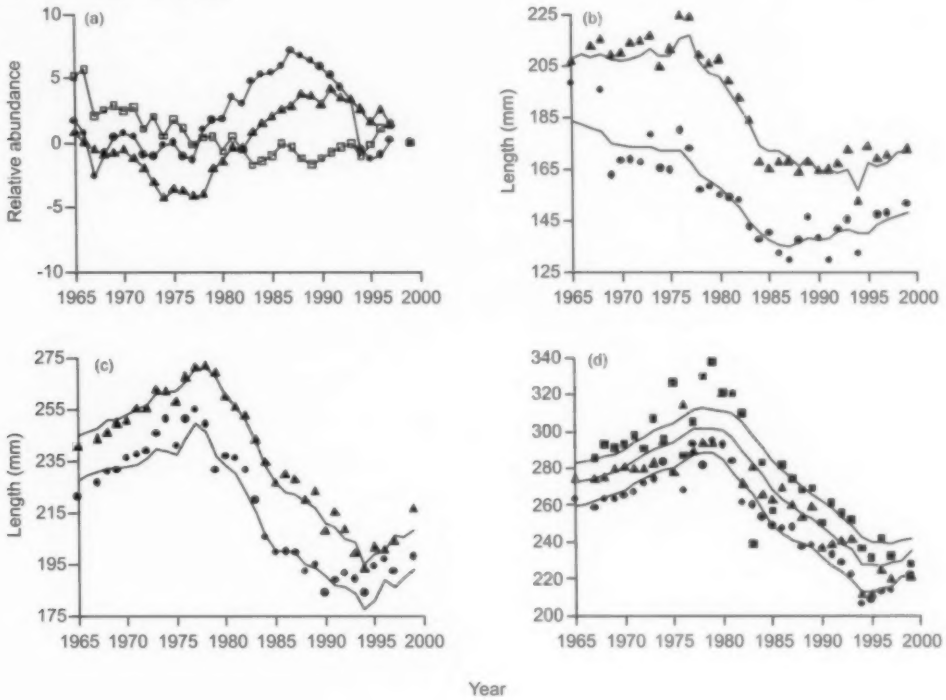
Fig. 1. (*a*) Relative abundance of yearling bloater (*Coregonus hoyi*) (solid circles), adult (age 2+) bloater (solid triangles), and adult alewife (*Alosa pseudoharengus*) (open squares) in Lake Michigan from 1965 to 1999. Observed (symbols) and predicted (lines) mean length-at-age for (*b*) age 1 (solid circles, lower line) and age 2 (solid triangles, upper line), (*c*) age 3 (solid circles, lower line) and age 4 (solid triangles, upper line), and (*d*) age 5 (solid circles, lower line), age 6 (solid triangles, middle line), and age 7 (solid squares, upper line) over time in Lake Michigan.



1967, three additional locations were included. Starting in 1973, an additional three locations were added for a total of seven fixed shore locations.

Bloater scales were collected annually for age determinations since 1965 (except for 1966 and 1998). Bloater scale sampling was limited to fish collected at four designated locations (Frankfort, Mich., Saugatuck, Mich., Waukegan, Ill., and Manistique, Mich.) rather than at all locations (except in 1999 when scales were also sampled from Ludington, Mich., and Port Washington, Wis.). From 1965 to 1982, scales were sampled from fish selected at random from the entire bloater size distribution at each of the designated locations. However, since 1983, scale samples have been collected following a stratified sampling design. Scales were collected from a maximum fixed number of fish for each 10-mm length class for each location sampled. The number of scale samples per length class sampled was not constant since 1983, but in most years, about 40 fish were sampled for scales from the most abundant length classes. As would be expected, in some years, very few individuals were sampled from both the smaller and larger length classes. Bloater ages were determined by visual inspection of projected scale images and an age class designation was based on enumeration of observed annuli. Bloater ranged from 0 to 12 years of age. Ageing error was not incorporated in the analysis of size-at-age data. Scored ages were assumed to be true ages for all fish. The amount of ageing error in scale ageing of bloater populations in the Great Lakes has not been investigated and studies of ageing error in other coregonid species have suggested that the amount of ageing error depends on growth rate, with higher error rates in slower-growing populations (Raitaniemi et al. 1998). Few individuals over age 7 were sampled, and scales were not consistently collected from individuals less than 100 mm in length. Thus, our growth modeling used data for ages 1 to 7 only.

Mean length- and weight-at-age

Because scale samples were not collected at all locations for the entire time period (1965–1999), it was not possible to calculate location-specific mean size-at-age. Previous analysis of the fall bottom trawl data has suggested that the mean size-at-age of bloater differs across the lake (Krause 1999). For this reason, bloater age data were pooled into a northern region (Port Washington, Wis., Sturgeon Bay, Wis., Manistique, Mich., Frankfort, Mich., and Ludington, Mich.) and southern region (Saugatuck, Mich., and Waukegan, Ill.) to calculate regional mean lengths- and weights-at-age (Fig. 2). Bloaters were sampled in both regions for all years except 1965 when only the southern region was surveyed. From 1965 to 1982, when age structures were sampled randomly, the mean length- and weight-at-age in each year and region were calculated by taking the mean of the length and weight, respectively, of all

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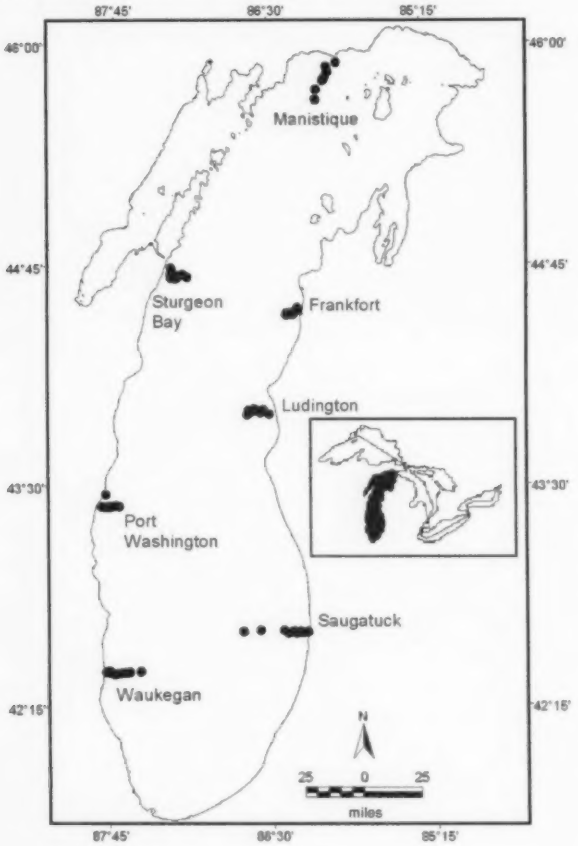
Fig. 2. Fixed shore locations in Lake Michigan for U.S. Geological Survey – Great Lakes Science Center fall bottom trawl survey. (Inset) Map of the Great Lakes with the international boundary between Canada and the United States of America indicated.



aged fish in each region. From 1983 to 1999 when stratified sampling was used, mean length-at-age ($\bar{L}_{a,y,i}$) in each year and region was estimated by

$$(1) \qquad \bar{L}_{a,y,i} = \frac{\sum_j p_{a,y,i,j}\, p_{y,i,j}\, \bar{l}_{a,y,i,j}}{\sum_j p_{a,y,i,j}\, p_{y,i,j}}$$

where $p_{y,i,j}$ is the proportion of the bloater in length bin j from the length–frequency sample for year y and region i, $p_{a,y,i,j}$ is the proportion of age a in length bin j from the scale sample for year y and region i, and $\bar{l}_{a,y,i,j}$ is the mean length-at-age a in length bin j for year y in region i (Gavaris and Gavaris 1983). For large catches (e.g., greater than 20 kg), the total size of the catch and the number of bloater in each length bin were estimated from subsamples of the total catch (see Krause (1999) for details). Mean weight-at-age ($\bar{W}_{a,y,i}$) in each region and year was estimated similarly with $\bar{l}_{a,y,i,j}$ replaced by $\bar{w}_{a,y,i,j}$ (mean weight-at-age a in length bin j in year y and region i). Because the bloater population is generally treated as one stock rather than as two distinct stocks, the regional estimates of size-at-age were averaged to obtain a lakewide estimate of mean size-at-age ($\bar{L}_{a,y}$ and $\bar{W}_{a,y}$, respectively) for the bloater population.

Abundance indices of bloater and alewife

CPUE data from the annual USGS fall trawl survey were analyzed to derive year-specific indices of relative abundance for adult (age 2+) bloater and alewife, along with yearling bloater. The natural log of the CPUE data was fit to a general linear model incorporating effects for year, location, and depth and allowing correlations among observations from the same location within a year (see Krause (1999)). The estimates of the fixed effects for year were used as an index of relative abundance. These relative indices are expressed on the natural logarithmic scale and differ from the natural log of CPUE by an additive constant. We used these indices to explore the relationship between the changes in bloater growth over time and abundance of yearling and adult bloater, along with adult alewife.

Growth model

We applied a growth model that allowed mean length-at-age to change between years. We also modeled the length–weight relationship in a way that allowed weight-at-length to vary over time. In combination, this allowed us to consider how both weight- and length-at-age changed over time. Dynamics in mean length-at-age were modeled by generalizing the incremental von Bertalanffy growth model to incorporate time-varying growth parameters. Thus, predicted mean length-at-age in a given year depended on mean length of the same cohort in the previous year and the growth parameters for the previous growing season. These predicted mean lengths-at-age were compared with the observed lengths-at-age over all years and adjustments in the growth parameters were made, using a numerical search, to provide the best agreement between the observed and predicted mean lengths-at-age. We were also interested in how the relationship between mean weight-at-age and mean length-at-age changed over time and thus modeled mean weight as a power function of mean length with parameters that were allowed to vary over time. The parameters determining this time-varying relationship were estimated by using them to predict mean weight-at-age using observed mean length-at-age and comparing these predictions to the observed mean weight-at-age. The parameters of the final model are described in Table 1. The dynamic equations used to predict mean length- and weight-at-age and changes in the growth parameters over time are described in Table 2. The equations presented in these tables are referenced by Tx.y, where x is the table number and y is the equation number within Table x.

Length-at-age model

In 1965, mean length-at-age for all ages was predicted by the standard form of the von Bertalanffy growth model (eq. T2.1). For all other years, mean length-at-age for ages 2 and older was predicted by the incremental form of the von Bertalanffy model (eq. T2.2). If the incremental form predicted a negative growth increment, then the growth increment was set to zero. This situation never occurred once the parameter values had converged to the best estimates. Because changes in yearling length over time could not be de-

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scribed well by the above model, we modeled yearling length separately as a random walk on the log scale (eq. T2.3). The random walk was started in 1965 at the yearling length predicted by eq. T2.1. This approach allows yearling length to change over time but assumes that yearling length in a given year would tend to be similar to the value from the previous year.

Similarly, we modeled L_∞ as a random walk on the log scale, where ε_y is a random change estimated by the model in every year and the random walk was started at L_∞ in 1965 (eq. T2.5). The parameters L_∞ and k were not allowed to vary freely from one another, rather k was assumed to be a linear function of L_∞ with a year-specific random (white noise) deviation (eq. T2.6). This relationship would allow L_∞ and k to have either a positive or negative relationship. The parameters of this relationship and each year-specific random deviation were estimated during the fitting process.

Weight-at-age model

Mean weight-at-age in every year was predicted from observed mean length-at-age ($\bar{L}_{a,y}$) using a length–weight relationship with time-varying parameters (eq. T2.4). Both α_y and β_y were assumed to follow a random walk on the log scale with the starting values in 1965 estimated as parameters during model fitting (eqs. T2.7 and T2.8, respectively).

Model optimization

The model was fitted using AD Model Builder software (Otter Research 2000). AD Model Builder is a superset of C++ that uses automatic differentiation in the application of a quasi-Newton method to fitting nonlinear models, based on a user-specified likelihood equation. In the fitting of this model, the negative log-likelihood function was minimized to obtain parameter estimates. The log-likelihood consisted of seven components:

$$(2) \qquad \ell = \ell_1 + \ell_2 + \ell_3 + \ell_4 + \ell_5 + \ell_6 + \ell_7$$

which correspond to those for the observed mean length- and weight-at-age, the random walks, and the white-noise deviations (Table 3). Mean length- and weight-at-age were both assumed to follow a lognormal distribution (eqs. T3.1 and T3.7). The random deviations from the random walks and from the relationship between L_∞ and k were assumed to follow normal distributions (eqs. T3.2–T3.6). Because the variance terms for ℓ_1–ℓ_7 were either estimated directly during model fitting or provided before fitting, the likelihood components are self-weighting and no additional weighting factors were used.

The variance term, $\sigma^2_{a,y}$, for ℓ_1 (eq. T3.1) was age- and year-specific and composed of two variance components, "measurement error", σ^2_m, and "process error", σ^2_p. The measurement error parameter captures the changes in the reliability of the mean lengths-at-age as sample size changes. The process error parameter captures any errors that are independent of sample size (e.g., the spatial distribution of certain sizes of bloater in the lake differing between years). The measurement error (on the log scale) was not fitted during the minimization process, rather an estimate was obtained based on the variation in observed lengths-at-age (σ^2_m = 0.0041) and treated as a constant.

For ℓ_4 (eq. T3.4), the variance term, σ^2_k, could not be estimated during model fitting at the same time as σ^2_∞. Both of these variances refer to process errors for unobserved state variables, and hence there is a singularity in the likelihood surface when their ratio approaches zero or infinity (Schnute and Richards 1995). As an alternative, we modified a strategy used by Schnute and Richards (1995). First we assumed that σ^2_k was proportional to σ^2_∞ with the proportionality constant, ρ, that was fixed before model fitting. During model fitting, σ^2_∞ was estimated as a parameter and the appropriate value of σ^2_k was calculated using the estimate of σ^2_∞ and the fixed value of ρ. To choose a value for ρ, we used an iterative approach. First, we fit the model using a wide range of values for ρ to obtain estimates of σ^2_∞ and σ^2_k. We also calculated the "observed" variances based on the variation in our estimates of ε_y and e_y for each value of ρ. By comparing the observed variances in the random deviations to the estimates of the variance components, we found there was only one value of ρ for which these quantities were approximately equal and used this value of ρ in our final model. At this value of ρ, the likelihood profile with respect to ρ is nearly flat. The resulting variances appeared reasonable to us and the resulting model predictions of mean length-at-age were not very sensitive to specific choices for ρ. Although our approach is a repeatable method for obtaining the ratio of these variances, it is an ad hoc approach. Methods for weighting likelihood components when process errors are involved is clearly an area for further research.

The variance components, σ^2_α and σ^2_β for ℓ_5 and ℓ_6 (eqs. T3.5 and T3.6, respectively), also could not both be estimated during the fitting process. Instead, as described for variance components of ℓ_4, we allowed σ^2_α to be estimated during the model fitting process and then assumed that σ^2_β was proportional to σ^2_α with a proportionality constant of φ that was fixed during model fitting. The value of φ was chosen using the same procedure described for ℓ_4.

The parameters L_∞, α, and β in the first year, the intercept of the linear relationship between L_∞ and k, and the variance components must be positive and were restricted to the positive real numbers during model fitting by estimating them on the log scale. All other parameters were estimated on the arithmetic scale.

Other model variants explored

The process of choosing the model structure presented above was based on exploring many variants of a standard von Bertalanffy growth model to find a model structure that adequately described the patterns found in the observed length- and weight-at-age data. We attempted to find the most parsimonious model that provided good predictions of mean size-at-age over time. We assessed model fit by visually inspecting residual plots and by using Akaike's information criterion (AIC) to compare different models. In this section we will describe several of the different model structures that we investigated to help guide model choice.

In an initial attempt to model the changes in length-at-age, we allowed only L_∞ to be different in each year, keeping k constant over the entire time period, which produced strong patterns in the residuals that we deemed unacceptable. Subsequently, we allowed both k and L_∞ to vary with time independently of one another, but this model failed to converge

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Table 1. Parameters and fixed constants for the time-varying von Bertalanffy growth model and weight–length relationship.

Parameter	Description
$L_{\infty_{1965}}$	L_∞ for mean length-at-age in 1965
ε_y	Random walk deviations for L_∞
t_0	Age at length 0 in 1965
b	Intercept of linear function between k and L_∞
m	Slope of linear function between k and L_∞
e_y	Year-specific deviations for linear function between k and L_∞
ξ_y	Random walk deviations for $L_{1,y}$
σ_m^2	"Measurement" error in length-at-age data*
σ_p^2	"Process" error in length-at-age data
σ_∞^2	Variance component for L_∞ random walk
σ_1^2	Variance component for $L_{1,y}$ random walk
ρ	Proportionality constant for variance component for e_y[a]
α_{1965}	α from the weight–length relationship in 1965
β_{1965}	β from the weight–length relationship in 1965
υ_y	Random walk deviations for α
δ_y	Random walk deviations for β
σ_w^2	Variance component for weight-at-age data
σ_α^2	Variance component for the α random walk
φ	Proportionality constant for the variance component of the β random walk[a]
n	Number of years
$n_{a,y}$	Sample size of fish aged in each age and year

[a]Parameter fixed during model-fitting process. See text for further explanation.

Table 2. Dynamic equations used to predict mean length- and weight-at-age and changes in growth parameters over time.

Mean length- and weight-at-age	
T2.1	$L_{a,1965} = L_{\infty_{1965}}(1 - e^{-k_{1965}(a-t_0)})$
T2.2	$L_{a+1,y+1} = L_{a,y} + (L_{\infty_y} - L_{a,y})(1 - e^{-k_y})$
T2.3	$\log(L_{1,y+1}) = \log(L_{1,y}) + \xi_y$
T2.4	$\hat{W}_{a,y} = \alpha_y \bar{L}_{a,y}^{\beta_y}$
Growth parameters	
T2.5	$\log(L_{\infty_{y+1}}) = \log(L_{\infty_y}) + \varepsilon_y$
T2.6	$k_y = b + mL_{\infty_y} + e_y$
T2.7	$\log(\alpha_{y+1}) = \log(\alpha_y) + \upsilon_y$
T2.8	$\log(\beta_{y+1}) = \log(\beta_y) + \delta_y$

Note: $L_{a,y}$ is the predicted mean length-at-age a in year y; $\bar{L}_{a,y}$ is the observed mean length-at-age a in year y; $\hat{W}_{a,y}$ is the predicted mean weight at observed mean length-at-age a in year y; L_{∞_y} is the asymptotic length in year y; k_y is the Brody growth coefficient in year y; and α_y and β_y are the parameters of the weight–length relationship in year y.

on a solution. In an attempt to allow both L_∞ and k to vary over time but in a correlated manner, we attempted to incorporate the functional relationships between L_∞ and k (of the general form $k = qL_\infty^{-g}$) proposed by Jensen (1996), but none of these models would converge on a solution, apparently because the assumed negative relationship does not agree with the observed data. We then fitted a model where k was a linear function L_∞, which was able to converge on a solution but still had strong patterns in the residuals, particularly for yearlings (age 1). To remove these patterns in the residuals, we arrived at the model presented above. We also attempted to capture the change in mean weight-at-age by allowing only α or β to vary with time, but we found that the AIC for the model in which both α and β were allowed to vary with time was lower than either of these simpler models.

Finally, we also fit a cohort-based model (i.e., growth parameters differed between cohorts but remained constant across a given cohort's life) because the growth patterns appeared to be correlated across years. However, we found that this model structure produced very strong patterns in the residuals and was unable to capture the changes in growth that occurred in the late 1990s. For this reason, we deemed this type of model unacceptable.

Results

Model fit

Although the measurement error variance (σ_m^2) was 6.81 times larger than the process error (σ_p^2; Table 4), the contribution of measurement error to total variance in predicted mean length-at-age declines rapidly with increasing sample size. For example, for a sample size of 10, the measurement error contributes ~40% to the total variance in predicted mean length-at-age, but its contribution declines to ~21% for a sample size of 25. Across all years and ages, 28% of the observed sample sizes (65 of 234 age–year samples) were

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Table 3. Log-likelihood components (ignoring constants) for bloater growth model.

T3.1	ℓ_1: mean length-at-age	$\sum_y \sum_a -0.5\left((\log(\sigma^2_{a,y}) + \frac{(\log(L_{a,y}) - \log(\bar{L}_{a,y}))^2}{\sigma^2_{a,y}}\right)$ $\sigma^2_{a,y} = \sigma^2_p + \sigma^2_m / n_{a,y}$
T3.2	ℓ_2: random walk in L_∞	$-\frac{n-1}{2}\log(\sigma^2_\infty) - \frac{0.5}{\sigma^2_\infty}\sum_y \varepsilon^2_y$
T3.3	ℓ_3: random walk in $L_{1,y}$	$-\frac{n-1}{2}\log(\sigma^2_1) - \frac{0.5}{\sigma^2_1}\sum_y \xi^2_y$
T3.4	ℓ_4: year-specific deviations in k	$-\frac{n}{2}\log(\sigma^2_k) - \frac{0.5}{\sigma^2_k}\sum_y e^2_y$
T3.5	ℓ_5: random walk in α	$-\frac{n-1}{2}\log(\sigma^2_\alpha) - \frac{0.5}{\sigma^2_\alpha}\sum_y \upsilon^2_y$
T.3.6	ℓ_6: random walk in β	$-\frac{n-1}{2}\log(\sigma^2_\beta) - \frac{0.5}{\sigma^2_\beta}\sum_y \delta^2_y$
T3.7	ℓ_7: mean weight at mean length	$\sum_y \sum_a -0.5\left(\log\left(\frac{\sigma^2_w}{n_{a,y}}\right) + \frac{(\log(\hat{W}_{a,y}) - \log(\bar{W}_{a,y}))^2}{\frac{\sigma^2_w}{n_{a,y}}}\right)$

Note: Parameters are defined in the text and Table 1.

less than 25. There was a higher percentage of sample sizes less than 25 in the yearling (33.3%) and older ages (age 5, 24%; age 6, 45%; age 7, 72%) than in the intermediate ages (age 2, 15%; age 3, 6%; and age 4, 3%). The model fit indicates a positive correlation between L_∞ and k (Table 3), implying that in years when L_∞ was high, k is also high (Fig. 3*c*). This result is contrary to many theoretical and empirical studies, which describe an inverse relation between L_∞ and k (Pauly 1980; Jensen 1996).

The residuals for both mean length-at-age and mean weight-at-age from this model were generally moderate in size, with most within ±2 standard deviations (SD), and only in three cases was the value outside the range ±3 SD. Moreover, the residuals generally exhibited no pattern with year at each age. We examined those specific cases in which there appeared to be a potential temporal pattern in the residuals. The first case was mean length-at-age 4, where there appeared to be a slight trend of negative residuals in the earlier years changing towards positive residuals in the later years. Because these residuals were relatively small in magnitude, they may simply represent a minor departure from the assumed von Bertalanffy growth model. We did not deem this minor departure of sufficient magnitude to explore a more flexible growth model such as the model proposed by Schnute (1981). The second and third cases, mean weight-at-ages 1 and 7, showed opposite trends. In predicting mean weight-at-age 1, the model slightly overestimated mean weight in the earlier years and underestimated it for later years in the series. For mean weight-at-age 7, the model tended to underestimate mean weight in the earlier years and overestimate it in later years. We interpret these results to indicate that our model may not have captured all of the complexities in changes in the bloater length–weight relationship over time and that the factors that influenced the weight at mean length of younger and older bloaters may be different.

Table 4. Parameter estimates and asymptotic standard errors (in parentheses) (φ = 18.16 and $\varphi = 2.75 \times 10^{-3}$).

Parameter	$\sigma^2_m = 0.0041$
t_0	–3.641 (0.477)
b	2.164×10^{-22} (7.65×10^{-17})
m	5.98×10^{-4} (7.68×10^{-5})
σ^2_p	7.40×10^{-4} (1.20×10^{-4})
σ^2_∞	4.51×10^{-5} (1.21×10^{-5})
σ^2_1	2.56×10^{-4} (1.03×10^{-4})
σ^2_w	0.199 (2.66×10^{-2})
σ^2_α	8.76×10^{-5} (3.18×10^{-5})

Note: This table contains all of the parameters that do not vary with time.

Bloater growth dynamics

The trends in estimates of both L_∞ and yearling length show a substantial decline over the latter portion of the study period (Figs. 1*b*, 3*a*). Estimates of L_∞ peaked in 1976–1977 at a value of 354 mm, then declined steadily through the 1980s and 1990s to 302 mm by 1999 (Fig. 3*a*). Yearling length declined from a maximum of 183 mm in 1965 to 135 mm in 1987 but subsequently has increased slightly (Fig. 1*b*). The estimates of k show a similar decline in the 1980s (Fig. 3*b*). Predicted and observed mean length-at-ages 2–7 showed an increasing mean length through the 1970s

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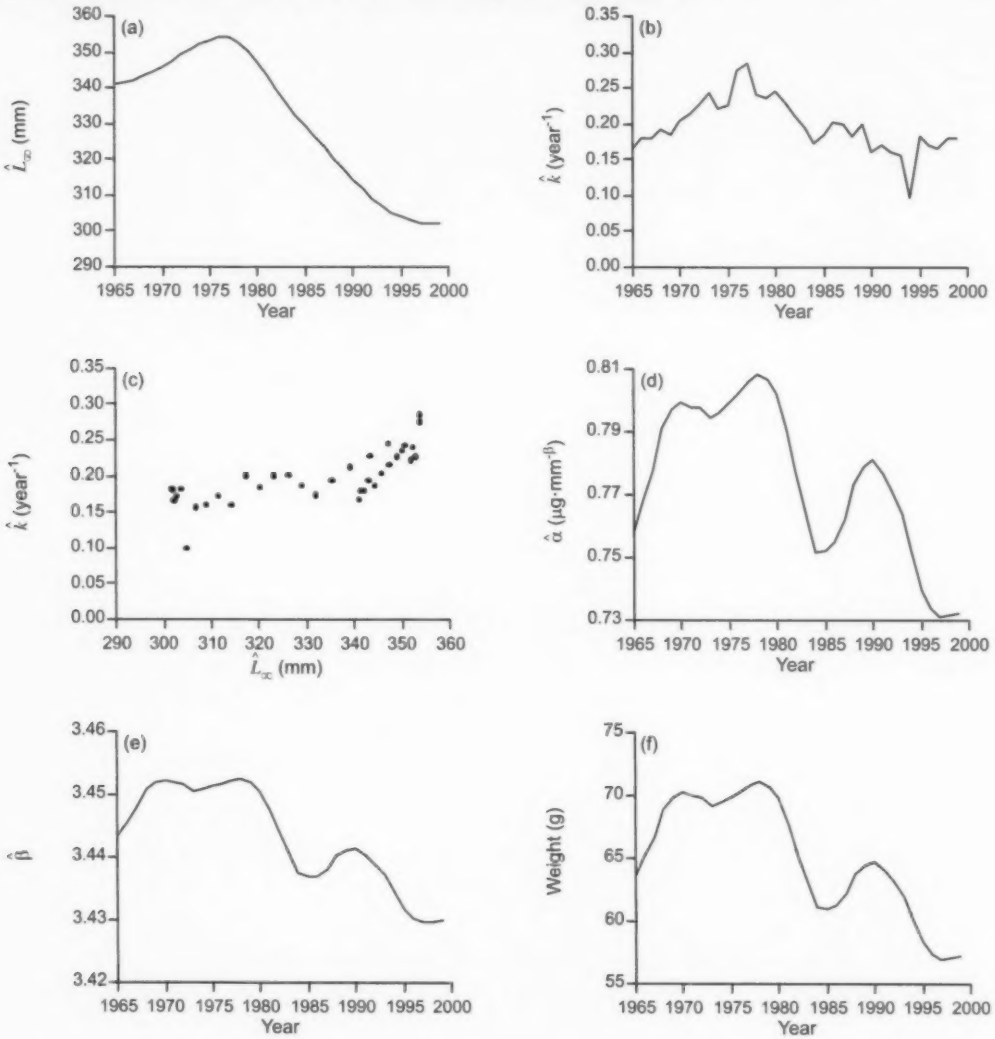
Fig. 3. Estimates of (*a*) L_∞, (*b*) k, (*d*) α, (*e*) β, and (*f*) predicted mean weight of a 200-mm bloater (*Coregonus hoyi*) over time. (*c*) The estimated relationship between k and L_∞ in the Lake Michigan bloater population.



and then declined sharply through the 1980s (Figs. 1*b*–1*d*). In recent years, mean length for all ages appears to be increasing slightly.

Estimates of α and β from the length–weight relationship show similar patterns of change over time (Figs. 3*d*, 3*e*). Both increased during the late 1960s and remained relatively high throughout the 1970s. During the 1980s they declined initially and then increased during the late 1980s before declining again in the 1990s. The predicted weight of an intermediate-sized bloater (200 mm) over time increased through the early 1980s and subsequently declined after a slight recovery in the early 1990s (Fig. 3*f*).

To assess the role that density-dependent mechanisms may play in regulating bloater growth, we graphically explored the relationships between the estimates of growth parameters and bloater population abundance. Estimates of L_∞ and the relative abundance of adult (age 2+) bloater appears to be inversely related during most of the study period (Fig. 4*a*). However, as adult bloater abundance peaked and then declined during the 1990s, estimates of L_∞ did not respond in an anticipated density-dependent fashion. In contrast, k shows a more regular linear decline with increased adult abundance (Fig. 4*b*) There appears to be a slight change in this trend at high relative adult abundance. If we factor out the effects of changes in L_∞ by only looking at the estimated random deviations (e_y), this feature is more apparent (Fig. 4*c*).

The temporal pattern in the bloater length–weight relationship through the mid-1980s also suggests density-dependent effects. Our estimates of the mean weight at 200 mm from 1965–1984 appear to follow a similar pattern with higher weight during periods of lower bloater abundance (Fig. 4*d*). However, during the late 1980s and early 1990s, mean weight increased despite the higher adult bloater abundances. This transient temporal response of mean weight at 200 mm was

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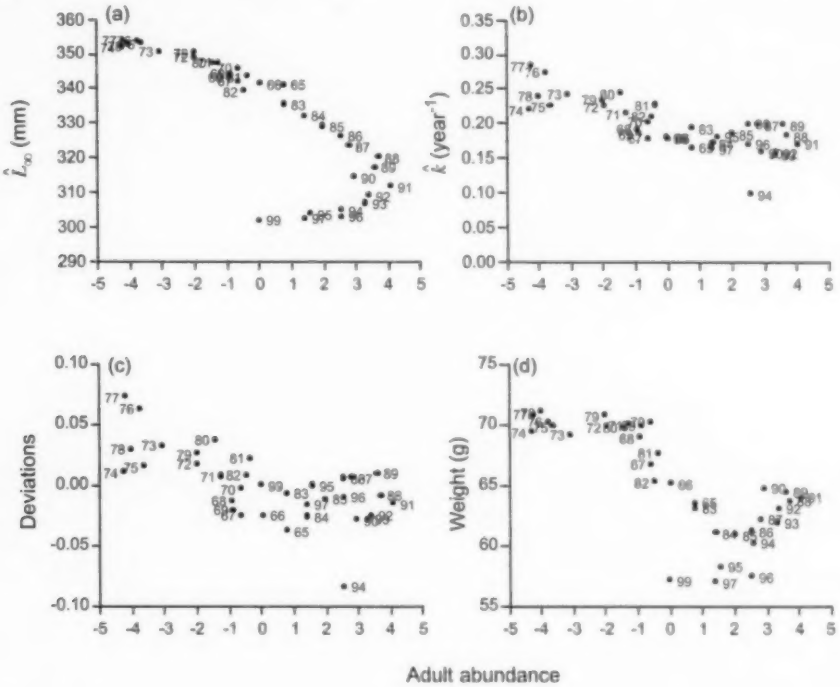
Fig. 4. Relationship between estimates of (*a*) L_∞, (*b*) k, and (*c*) deviations (e_y) from the linear relationship between L_∞ and k and (*d*) predicted mean weight of a 200-mm bloater (*Coregonus hoyi*) and the relative abundance of adult (age 2+) bloater in Lake Michigan, 1965–1999.



not seen in the von Bertalanffy parameters. Subsequently, mean weight at 200 mm returned to low levels and, like L_∞, did not increase in the late 1990s despite lower bloater abundance.

Density-dependent growth also appears to occur for yearling bloaters. The relationship between estimated yearling length and yearling relative abundance shows decreased yearling size with increased abundance of yearlings (Fig. 5*a*). However, in the most recent years (1994–1999), as was seen for the adult growth parameters, this relationship appears to have broken down. Juvenile bloater growth and adult alewife abundance are positively correlated from 1965 to 1999, with larger yearling length achieved in times of high alewife abundance (Fig. 5*b*).

Discussion

We were able to capture the dramatic changes in bloater size-at-age by modeling changes in L_∞, k, α, β, and yearling length. The model, in general, predicted mean length- and weight-at-age that agreed very well with observed data. Some patterns were detected in the residuals, but these patterns appear to be only minor deviations from our growth model. Although limits with regard to estimability were encountered (e.g., we could not estimate k independently for each year), we were still able to capture the dynamics and infer the mechanisms of the changes in bloater growth over time.

Our model shares features with some previous attempts to fit dynamic growth models to mean length-at-age data (Millar and Myers 1990; Millar et al. 1999). Unique features of our approach included using a time series approach to describe changes in growth parameters over time (i.e., random walks) rather than assuming relationships with environmental factors and combining length- and weight-at-age information in the description of changes in growth over time. By using a dynamic growth model, such as the model presented here, the noise inherent in mean size-at-age data can be smoothed, eliminating the negative growth increments that are often observed when calculated directly from observed size-at-age. Furthermore, the parameters of the growth model provide a useful and parsimonious way of summarizing how growth is changing over time and allow researchers to investigate mechanisms for changes in growth over time using information from all ages rather than a selected few.

The incremental growth model presented here allowed all fish of the same size, regardless of their previous growth history, to achieve the same growth. This feature allowed for fish to recoup size-at-age even after previous poor growth if conditions improved. As such, this model would not be able to emulate stunting (the phenomenon of previous growth history influencing current growth potential; Ylikarjula et al. 1999). Although we did not see evidence for stunting in the Lake Michigan bloater population, our ability to detect this condition may be obscured because of the relatively slow change in conditions over time and the observation that most individuals experiencing poor growth conditions in early life also experience poor growth conditions as an adult. If further evidence suggests that stunting may be important in bloater growth dynamics, then the dynamic growth model would need to be adjusted to incorporate this process. Millar and

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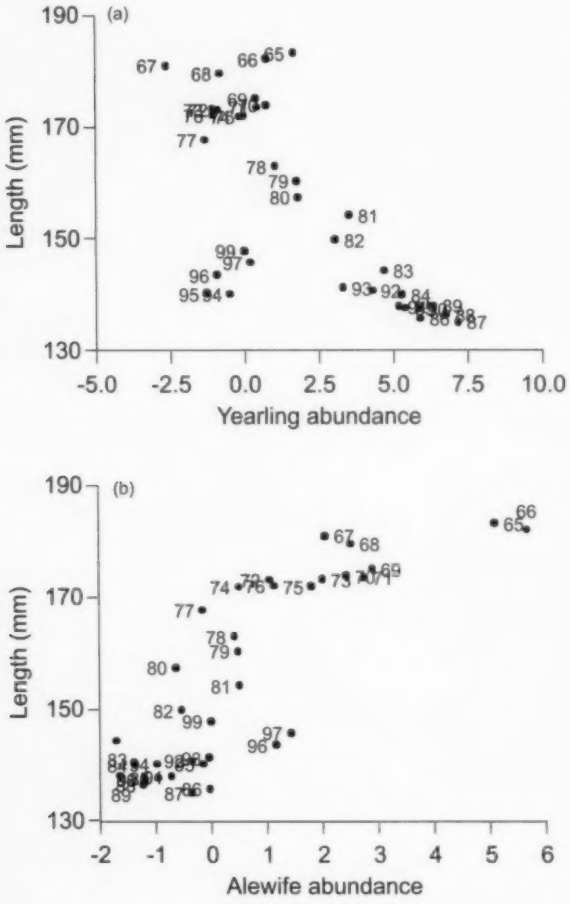
Fig. 5. Relationship between estimated yearling length and (*a*) relative abundance of yearling bloater (*Coregonus hoyi*) in Lake Michigan, 1965–1999, and (*b*) relative abundance of adult (age 2+) alewife (*Alosa pseudoharengus*) in Lake Michigan, 1965–1999.



Myers (1990) have explored one model that incorporates stunting and could be used in an analysis similar to ours.

Our analysis indicates a positive relationship between L_∞ and k in the Lake Michigan bloater population. Previous studies of fish growth have shown that the relationship between L_∞ and k is generally negative (Pauly 1980; Jensen 1996). However, Pauly (1980) looked at this relationship across populations, whereas we looked within one individual fish population. We have tried several functional forms to force a negative relationship between L_∞ and k; however, none of these models was able to converge on a solution. The positive relationship that we observed, although initially counterintuitive, simply implies that when growth conditions are favorable for bloaters, they respond with both fast growth rates and larger maximum sizes.

Our analysis corroborates a previously reported density-dependent growth response of bloater in Lake Michigan (TeWinkel et al. 2002). All of the growth parameters estimated seemed to decline in concert with increasing bloater abundance. However, since the beginning of the 1990s, a change in this relationship appears to have occurred. During this time, bloater growth in length and mean weight at 200 mm remained low despite relatively low abundances of both adult and juvenile bloater. We note that these recent changes in bloater growth were coincident with the invasion and expansion of zebra mussels (*Dreissena polymorpha*) and the disappearance of *Diporeia* spp. in Lake Michigan (Nalepa et al. 2000; Fleischer et al. 2001). *Diporeia* represents a major link between pelagic production and upper trophic levels in Lake Michigan and is also an important component of adult bloater diet in Lake Michigan, exhibiting higher lipid content than other benthic macroinvertebrates (Gardner et al. 1985; Rand et al. 1995; Davis et al. 1997). Zebra mussels may also be having profound effects on the primary productivity of Lake Michigan because of energetic demands (Madenjian 1995; Stoekmann and Garton 1997) that may manifest in lower productivity in lower trophic level fishes.

Interestingly, the changes in bloater growth in the 1990s are evident in the estimates of L_∞ and yearling length but not in the estimates of k. This suggests that although all three growth parameters may be affected by intraspecific density, changes in the food web can influence them differently. Such a difference could arise if the change in the food web caused approximately the same effect on incremental growth (in length), irrespective of fish size (see Walters and Post 1993). Only future monitoring of bloater length-at-age will tell if these trends continue in the future and if these changes in bloater growth are a harbinger of future changes to the Lake Michigan ecosystem.

Our inability to model changes in growth of both adult and juvenile bloater with a common set of parameters suggests that these life stages of bloater may be responding to different environmental conditions. This result is not unexpected because of the different bathymetric habitats occupied by the two life stages. Juvenile bloater occupy more nearshore, shallower depths and feed primarily on zooplankton, whereas adult bloater are limited to a hypolimnetic distribution and feed primarily on hypolimnetic prey (Davis et al. 1997). Consequently, intraspecific density-dependent growth in bloaters appears to be life stage specific (i.e., juvenile growth appears to respond strongly to juvenile abundance but not to adult abundance, and adult growth seems to respond primarily to adult abundance).

Previous studies have concluded that the invasion of the exotic alewife (*Alosa pseudoharengus*) has had profound effects on the bloater population in Lake Michigan (e.g., Crowder and Crawford 1984; Eck and Wells 1987). For example, Crowder and Crawford (1984) suggested that competition between the pelagic juvenile bloater and adult alewife for pelagic resources has caused bloater to switch to benthic resources at an earlier age (from age 3 to age 2). If competition between juvenile bloater and adult alewife was strong, we would expect that in times of high alewife abundance, juvenile bloater growth would be reduced. In fact, young bloater growth rate, as indicated by predicted yearling length, increased in concert with adult alewife abundance. This suggests that any negative interaction between juvenile bloater and adult alewife does not appear to affect juvenile

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bloater length, at least within the densities of alewife and bloater observed during the study period (1965–1999).

The implications of density-dependent growth in bloater for the Lake Michigan ecosystem may be profound. Since the mid-1980s, concern about the balance between the predatory demands of stocked salmonids and the productivity of the forage base has risen. Several observations indicate that the forage available to the salmonids, particularly the chinook salmon (*Oncorhynchus tshawytscha*), may not be sufficient to maintain the large populations of the 1980s (Stewart and Ibarra 1991; Holey et al. 1995). Bloater, especially smaller individuals, represent a potentially important alternative forage item for the salmonids (Madenjian et al. 1998). Therefore, in the future, an understanding of the forces governing bloater dynamics will be important in balancing predatory demand and forage availability. Changes in size-at-age may have many effects on their population dynamics, including mortality rates and fecundity. Our ability to accurately assess the availability of forage for salmonids depends in part on our understanding of bloater population dynamics.

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Performance of indicators derived from abundance estimates for detecting the impact of fishing on a fish community

Verena M. Trenkel and Marie-Joëlle Rochet

Abstract: Population and community indicators for the impact of fishing are often estimated using abundance estimates instead of raw sampling observations. Methods are presented for testing null hypotheses of nonsignificant impacts and, where possible, for calculating the statistical power. The indicators considered concern populations (intrinsic growth rate, total mortality, exploitation rate, and a new indicator, the change in fishing mortality required to reverse population growth) and communities (k- and partial-dominance curves, a biodiversity index, size spectrum, and proportions of various population groups). The performance of these indicators is compared for the Celtic Sea groundfish community based on achieved precision, statistical power, and availability and estimation method of reference points. Among population indicators, mean length of catch was most precisely estimated and the corresponding hypothesis tests had consistently large powers. Total mortality performed reasonably well. In contrast, both the intrinsic population growth rate and the exploitation rate gave unreliable results. All tested community indicators performed similarly well. Indicators for which the direction of change caused by fishing is predictable, such as the proportion of noncommercial species or piscivores in the community, are promising indicators at the community level.

Résumé : Les indicateurs de l'impact de la pêche sur les populations et les communautés sont souvent estimés à partir d'estimations d'abondance, et non directement d'observations issues de l'échantillonnage. Cet article présente des méthodes pour tester l'hypothèse nulle d'absence d'impact dans ce genre de situation, ainsi que pour calculer la puissance de ces tests quand c'est possible. Les indicateurs considérés concernent les populations (taux de croissance intrinsèque, mortalité totale, taux d'exploitation et un nouvel indicateur, le changement de mortalité par pêche nécessaire pour inverser la tendance de la population) et les peuplements (courbes de k-dominance et de dominance partielle, un indice de diversité, le spectre de taille multispécifique et les proportions de divers groupes de populations). Les performances de ces indicateurs pour évaluer l'impact de la pêche sur le peuplement de poissons de fond de la mer Celtique sont comparées, en termes de précision, de puissance et de la possibilité d'estimer un point de référence. Parmi les indicateurs de population, la longueur moyenne dans la population est l'indicateur estimé avec la meilleure précision et les tests correspondants ont une puissance élevée. La mortalité totale montre des résultats intermédiaires, alors que le taux de croissance intrinsèque de la population et le taux d'exploitation sont peu fiables. Tous les indicateurs de peuplement examinés rencontrent un succès comparable. Pour ce niveau d'organisation, les indicateurs pour lesquels la direction du changement causé par la pêche est prévisible, comme la proportion d'espèces non-commerciales ou piscivores, sont des indicateurs prometteurs.

Introduction

Assessing the impact of fishing on different components of the ecosystem is an important part of recent attempts to introduce ecosystem consideration into fisheries management (Anonymous 1999; Hall 1999; ICES 2000). Various indicators have been proposed for measuring the direct and indirect impacts on fish and benthic communities (FAO 1999; Rice 2000; Rochet and Trenkel 2003). In this paper we compare the performance of selected indicators applied to French groundfish survey data for the Celtic Sea using three statistical criteria: estimation precision, achieved testing power (if available), and availability and estimation method of reference points. Until now, indicators have mainly been assessed based on theoretical considerations (Rice 2000; Rochet and Trenkel 2003), which is only part of the story. Although the data series for the Celtic Sea is only 4 years long, we believe that it provides a typical example of many situations confronting fisheries scientists. We simply cannot afford to wait 20 years before establishing a system diagnosis!

The ecological theory underpinning certain indicators allows the determination of reference points that can be targets or limits and express the null hypothesis of a system not unduly influenced by fishing. Measurable impacts of fishing are affirmed if the indicator value for a community of interest is above or below the limit reference point or far from the target reference point. In the context of sustainable de-

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Table 1. Indicators for measuring the impact of fishing on population i.

Indicator	Description	Required information	Model	Estimation method
r_i	Intrinsic population growth rate	$N_i(t)$	(1) $N_i(t) = N_i(t-1)\exp(r_i) = \lambda_i N_i(t-1)$	$\log(\hat{N}_i(t)) = \delta_i + r_i t + \omega_{i,t}$ $\omega_{i,t} \sim N(0, \sigma_i^2)$
Z_i	Total mortality	$N_{l,i}(t)$, t_{0_i} k_i, L_{∞_i}	(2) Cohort $N_i(t) = N_i(0)\exp(-z_i t)$ $N_{l,i}(t) =$ $\exp\left(\ln(N_i(0) - Z_i\left(t_{0_i} - \frac{1}{k_i}\ln\left(1 - \frac{l_l}{L_{\infty_i}}\right)\right)\right)$	GLM: log-link, quasi-likelihood with var $\propto$ mean$^{\beta_i}$
F_i/Z_i	Exploitation rate	$C_i(t)$, $N_i(t)$, Z_i	(3a) $F_i(t) = C_i(t)/N_i(t)$	(3b) $\hat{F}_i(t) = \hat{C}_i(t)/\hat{N}_i(t)$ $\hat{V}[F_i(t)] = \hat{V}[C_i(t)]/\hat{N}_i(t)^2$ $+ \hat{C}_i(t)^2\ \hat{V}[N_i(t)]/\hat{N}_i(t)^4$ (Kendall and Stuart 1977)
L_{bar_i}	Mean length of catch	$C_{l,i}$	(4) $L_{\text{bar}_i} = \frac{1}{C_i}\sum_{l=1}^{L} C_{l,i}\, l_l$	$\hat{L}_{\text{bar}} = \frac{1}{\hat{C}_i}\sum_{l=1}^{L}\hat{C}_{l,i}\, l_l$ $\hat{V}\left[\hat{L}_{\text{bar}_i}\right] = \hat{L}^2_{\text{bar}_i}$ $\times\left(\frac{\sum_{l=1}^{L} l_l^2\ \hat{V}[\hat{C}_{l,i}]}{\left(\sum_{l=1}^{L} l_l \hat{C}_{l,i}\right)^2} + \frac{\hat{V}[\hat{C}_i]}{\hat{C}_i^2}\right)$
ΔF_i	Change in F to reverse population growth	F_i, Z_i, α_i, λ_i	(5) $\Delta F_i = \exp(\Delta r / e_F - 1)$ $e_F = \frac{F_i}{\lambda_i}\frac{\lambda_i \exp(-Z_i)}{\alpha_i \exp(-Z_i) - \lambda_i(1+\alpha_i)}$ $\lambda_i = \exp(r_i)$	$\hat{e}_F = \frac{\hat{F}_i}{\hat{\lambda}_i}\frac{\hat{\lambda}_i \exp(-\hat{Z}_i)}{\alpha_i \exp(-\hat{Z}_i) - \hat{\lambda}_i(1+\alpha_i)}$ $\hat{\lambda}_i = \exp(\hat{r}_i + V[\hat{r}_i]/2)$ $\hat{\Delta r} =$ lower CI$(\hat{r}_i)$

Note: Null hypotheses represent no measurable impact of fishing. CI, confidence interval; $N_i(t)$, total abundance of species i; k_i and L_{∞_i}, parameters of maturity; L_{c_i}, length at first capture; α_i, age at maturity; l_l, length of length class l; L, number of length classes; e_F, elasticity of λ to F.

velopments of marine capture fisheries promoted by the United Nations Food and Agriculture Organization (FAO; e.g., Garcia et al. 2000), target or limit reference points might be defined in accordance with some agreed management objectives and might admit system changes to some degree. The principal aim is to guide management and to reconcile multiple uses. In contrast, the indicators and their respective reference points discussed in this paper are intended to allow objective detection of changes that could have been caused by fishing. In terms of management objectives, the chosen reference points translate into no system changes allowed. Management actions to ensue might not be obvious as the link between fishing activity and community indicator are not clearly established in contrast to some population indicators such as the fishing mortality rate (see also discussion in Rochet and Trenkel 2003).

For a number of indicators, no theory exists that allows the definition of reference points or even the range of acceptable indicator values. Hence, one must look for consistent changes over time that might indicate the impact of fishing. Evidence for the presence of fishing impacts will be provided by simultaneous rejection of null hypotheses for several indicators intended to provide information on similar aspects. However, as fishing impact is assessed against a background of natural environmental fluctuations and changes, identification of the most important driving factor might be difficult or impossible.

Direct comparison of indicator values with reference points is only possible in the uncommon case of fully censused communities. In general, communities have to be sampled. To obtain conclusions about the community, inference has to be drawn within a hypothesis-testing framework where reference points or no change are taken as null hypotheses. The alternative hypotheses are that indicators are above or below the respective limit reference point or show a consistent trend over time resulting from the impact of fishing and (or) long-term environmental changes.

Most existing indicators are based on estimates or observations of population abundances generally obtained from research vessel surveys. If random samples from the community have been taken, then the empirical sampling distribution of an indicator can be used directly for hypothesis testing. Furthermore, randomization tests rearranging the spatial or temporal origin of individual samples can be used for comparing years and areas (Clarke 1990) and for comparing patterns to null models, which assume similar structures

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Null hypothesis H_0	H_0 reference	Indicator distribution	Hypothesis test method
$r_i = 0$		Normal	0 within 95% CI of $\hat{r}_i$
$Z_i < Z_i^* = \frac{(L_{\infty_i} - L_{\mathrm{mat}_i})k_i}{L_{\mathrm{mat}_i} - L_{c_i}}$	Die and Caddy (1997)	Normal	Z_i^* above 95 percentile point of $\hat{Z}_i$
$F_i/Z_i < 0.5$	Alverson and Pereyra (1969)	Normal	0.5 above 95 percentile point of $\hat{F}_i/\hat{Z}_i$
$L_{\mathrm{bar}_i} > L_{\mathrm{mat}_i}$	Caddy and Mahon (1995)	Normal (central limit theorem)	L_{mat_i} below 5 percentile point of $\hat{L}_{\mathrm{bar}_i}$
$\Delta F_i\% > 20\%$	Rochet and Trenkel (2003)	Unknown	$\hat{\Delta} F_i\% > 20\%$

von Bertalanffy growth model; l, length class; $C_i(t)$, total catch (discards + landings); $C_{l,i}$, catch in length class l; F_i, fishing mortality; L_{mat_i}, length at

(Veech 2000). An application of these methods to the groundfish community of the northern North Sea can be found in Greenstreet and Hall (1996).

In the case of stratified, adaptive, or nonrandom sampling designs, the raw (haul) data do not form a representative sample of the studied community. Instead, abundance estimates by species have to be calculated giving appropriate weights to each sample. As a consequence, empirical sampling distributions of indicators are not available and simple randomization cannot be carried out.

For a selection of commonly used indicators, we propose methods for obtaining indicator sampling distributions and carrying out hypothesis tests when the indicators have been estimated using abundance estimates. The selected indicators fall into two categories: indicators measuring the state and dynamics of individual populations and indicators for the community structure and functioning (Tables 1 and 2). To the best of our knowledge, their sampling distributions derived from abundance estimates have not been studied to date.

We decompose the process of hypothesis testing into several tasks. First, data requirements are examined (Tables 1 and 2) and data sources for estimating indicators and their reference points are summarized (Table 3). Most indicators dealt with in this study are based on annual abundance estimates by species, $N_i(t)$, or by length group and species, $N_{l,i}(t)$. Second, appropriate abundance estimators are chosen and their distributions are determined. Third, given the definition of indicators and the distribution of the input information, appropriate estimation methods are selected for indicators that represent model parameters, for example, the intrinsic population growth rate r, which is a parameter of a simple population dynamics model. If the estimation method makes parametric assumptions, such as normality for linear regression, the actual distribution of the input information is checked. Fourth, given the sampling distributions of abundance estimates and appropriate estimation methods, the resulting distributions of indicator estimates are studied. Hypothesis tests are carried out for indicators with reference points; linear time trends are tested for the other indicators. If possible, the statistical power of hypothesis tests is estimated.

Methods

Abundance estimation

Generally, fish numbers per haul have strongly skewed dis-

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tributions. The question of which estimator to use for obtaining abundance estimates, in this case, has attracted attention from several authors. Pennington (1983) states that estimators based on the lognormal distribution are more efficient than estimates based on sample means. However, based on a simulation study, Myers and Pepin (1990) recommend using lognormal-based estimators only if the lognormal distribution assumption for nonzero observations is justified, as these estimators are sensitive to assumption violations. Hence, it is advisable to test the distribution of numbers per haul.

For the Celtic Sea groundfish community, two examples of empirical distributions of observed numbers per haul show strong skewness and long right-hand tails (Fig. 1). Empirical distributions for all strata and years for which a reasonable number of hauls ($n > 15$) was available were compared with gamma, normal, and lognormal (nonzero observations only) distributions (χ^2 tests); none of the distributions could be rejected as being inappropriate for any of the tested species.

If the appropriateness of the lognormal distribution cannot be confirmed as in our example, we propose to follow the advice given by Myers and Pepin (1990) and use simple mean-based sample estimators. For the Celtic Sea, for each species i (or length class), this involves dividing the mean per stratum (including hauls where the species was not observed) by the swept area, multiplying by the stratum area, and then summing over all strata. This gives abundance estimates $\hat{N}_i$. Variances $\hat{V}[\hat{N}_i]$ are estimated correspondingly.

Looking at the relationship between abundance estimates $\hat{N}_i$ and their variances $\hat{V}[\hat{N}_i]$ is a second way of trying to identify the distribution of abundance estimates. For this the slope of the linear regression of $\log(\hat{V}[\hat{N}(t)])$ on $\log(\hat{N}(t))$ is estimated. In our example, we found that $V[\hat{N}] \propto \hat{N}^2$ for most species by testing for slopes equal to two. Two observations can be made: (*i*) abundance estimates are heteroscedastic; (*ii*) gamma and lognormal distributions exhibit this particular mean–variance relationship. Hence, either of them could be used to describe the distribution of estimated abundances. For certain estimation methods we do not need to know the full distribution. It is sufficient to stabilize variances, which can be achieved by log transformations. Normal error distributions are then appropriate for the log-transformed abundance estimates.

Abundance indices are relative measures of population numbers; a factor of proportionality stands between the two. This factor of proportionality differs between species and is often referred to as catchability, which can be assumed constant as long as the survey setup remains unchanged. If estimates of catchability are available, abundance indices can be corrected. In our case, no catchability estimates were available and catchabilities of 1 were assumed for all species. The effect of this assumption is that indicators involving more than one species will represent the part of the community accessible to the survey gear rather than the real community.

Estimation, sampling distributions, and hypothesis tests

Indicator estimation methods are divided into population indicators (Table 1, column 5) and community indicators (Table 2, column 3). In the following we briefly review all indicators, explain estimation methods that differ from standard use, and comment on their reference points.

Intrinsic population growth rate (r)

The intrinsic population growth rate is estimated using annual population abundance estimates. The population dynamics model underlying this indicator can be linearised by taking logarithms of both sides (Table 1, eq. 1). As the log transformation is also applied to abundance estimates, the transformation stabilizes variances and justifies the use of standard regression techniques for estimating r as the slope. However, in the transformed model, residuals are serially correlated as the independent variables form a time series. We can take account of this by formulating a first-order autoregressive model for residuals, which requires a time series with a certain number of years, as three parameters have to be estimated. Hence, for our case study we use simple linear regression. Taking $r = 0$ as the target reference point assumes that without any noticeable impact of fishing, the population would be stable although varying between years.

Total mortality rate (Z)

The estimation method for total mortality is based on a simple population dynamics model for a given cohort. The age-based model is transformed into a length-based model using the von Bertalanffy growth function (Table 1, eq. 2). To use estimated numbers at length for a given year instead of a cohort, it is assumed that recruitment has been constant in the past in addition to a constant total mortality rate, the later assumption implying constant fishing pressure. Hence this method is most valid when the intrinsic population growth rate is zero. If the assumptions are appropriate, similar Z estimates should be obtained for different years and r should not be significantly different from zero. Z could be estimated by linear regression of the log-transformed model. The alternative is to avoid the normality assumption of linear regression and use a generalized linear model with log-link and quasi-likelihood function. We chose the second approach. The limit reference point Z^* is derived from expressing total mortality as a function of asymptotic length L_∞, length at maturity (L_{mat}), and length at first capture (L_c) (Die and Caddy 1997). To obtain reliable estimates of L_c, we used the first 5-cm length class accounting for at least 10% of the total catch.

Exploitation rate (F/Z)

Fishing mortality F is estimated from catch data (landings and discards) and estimated population abundance (Table 1, eq. 3*a*). Total mortality Z is estimated as the average of annual estimates. For the Celtic Sea, we only have discard data for 1997 and hence estimate fishing mortality for that year only. Variances of both F and F/Z have been estimated using the delta method (Table 1, eq. 3*b*). The limit reference point $F/Z = 0.5$, which represents an upper limit, was proposed based on production considerations (Alverson and Pereyra 1969; see also discussion in Rochet and Trenkel 2003).

Mean length of catch (L_{bar})

A suitable indicator would be the median length of catch (L_{median}), which should be above L_{mat} to give at least half of the individuals of a cohort a chance to reproduce. However, the distribution of the median is not well known; only its variance can be easily estimated. The alternative is to use mean length of catch L_{bar}, provided that the mean and

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Table 2. Indicators and their data requirements for measuring the impact of fishing on a community consisting of S species ($i = 1,\ldots, S$).

Indicator	Required information	Estimator	Method to obtain indicator distribution	Null hypothesis	Alternative hypothesis	Hypothesis test method
Δ_1	$N_i(t)$	(6) $\hat{\Delta}_1 = \frac{\hat{N}}{\hat{N}-1}\left[1 - \sum_{i=1}^{S}\left(\frac{\hat{N}_i}{\hat{N}}\right)^2\right]$ $\hat{V}[\hat{\Delta}_1] \approx \sum_{i=1}^{S}\hat{V}[\hat{N}_i]\left(\frac{2\hat{N}_i}{\hat{N}^2} - \sum_i \frac{2\hat{N}_i^2}{\hat{N}^3}\right)$	Parametric bootstrap of abundance estimates	No change	Increase or decrease	Overlapping 95% CI
k-dominance curve	$N_i(t)$	(7) $D_i = \sum_{i=1}^{i}\hat{N}_i/\hat{N}, \quad N_i > N_{i+1}$	Parametric bootstrap of abundance estimates	No change	—	Rank-wise comparison of CI
Partial dominance curve	$N_i(t)$	(8) $D_k = \hat{N}_k/\sum_{i=k}^{S}\hat{N}_i, \quad N_i \le N_k$	Parametric bootstrap of abundance estimates	No change	—	Rank-wise comparison of CI
Species composition	$N_i(t)$			Species abundances similar in all years	Years are different	Slope of Euclidian distances regressed against square root of time lag
Proportion of non-commercial species	$B(t)$, $B_n(t)$ $N(t)$, $N_n(t)$	(9) $\hat{B}_n(t)/\hat{B}(t)$ (10) $\hat{N}_n(t)/\hat{N}(t)$	Parametric bootstrap of biomass–abundance estimates; GLM binomial distribution with logit-link	$\text{logit}(N_n(t)/N(t)) = a + ct$, $c = 0$	Increase in proportion of noncommercial species, $c > 0$	Empirical bootstrap distribution of time effect
Distribution of mean population length	$\bar{L}_i$	$\hat{\bar{L}}_i = \frac{1}{\hat{N}_i}\sum_{l=l_{mat}}^{l} l\hat{N}_{i,l}$		No change	Shift to smaller sizes	Nonparametric Kolmogorov–Smirnov test
Size–abundance relationship	$N_i(t)$, $\bar{L}_i(t)$	(11) LM: $\log(\hat{N}) = a + b\log(\hat{\bar{L}})$	Normal distribution assumptions	$b = 0$, no trend	$b \neq 0$	F test
Total biomass Total numbers	$B(t)$ $N(t)$	(12) $\hat{B}(t) = \sum_i B_i(t)$	Unknown	$B(t) = a + ct$, $c = 0$, no trend	$c \neq 0$	Robust regression for time effect
Proportion of piscivores	$B(t)$, $B_p(t)$ $N(t)$, $N_p(t)$	(13) $\hat{B}_p(t)/\hat{B}(t)$ $\hat{N}_p(t)/\hat{N}(t)$	Parametric bootstrap of biomass–abundance estimates; GLM binomial distribution with logit-link	$\text{logit}(N_p(t)/N(t)) = a + ct$, $c = 0$	Decrease in proportion of piscivores, $c < 0$	Empirical bootstrap distribution of time effect
Average individual weight (community) length (community)	$\bar{b}(t)$ $\bar{l}(t)$	(14) $\hat{\bar{b}}(t) = \hat{B}(t)/\hat{N}(t)$	Normal distribution assumption	$\bar{b}(t) = a + st$, $s = 0$, no trend	$s \neq 0$	Linear regression $V[\hat{s}] = (t't)^{-1}\bar{V}[\hat{\bar{b}}(t)]$
Size spectrum	$N_l(t)$	(15) GLM: $N_l(t) = a_t \exp(b_t(l_l - \bar{l}))$	Unknown	$a_t = a$ $b_t = b$ No year effect	$a_t \neq a$ $b_t \neq b$	Model comparison by log-likelihood ratio tests

Note: Null hypotheses represent no measurable impact of fishing or no change. CI, confidence interval; LM, linear regression; N_i, abundance of species i; B, biomass; $\bar{L}_i$, mean length of species i (mature animals); N_l, numbers in length class l; l_l, length of length class l; M, natural mortality; F, fishing mortality; r, intrinsic population growth rate; t, year; n, noncommercial; p, piscivores.

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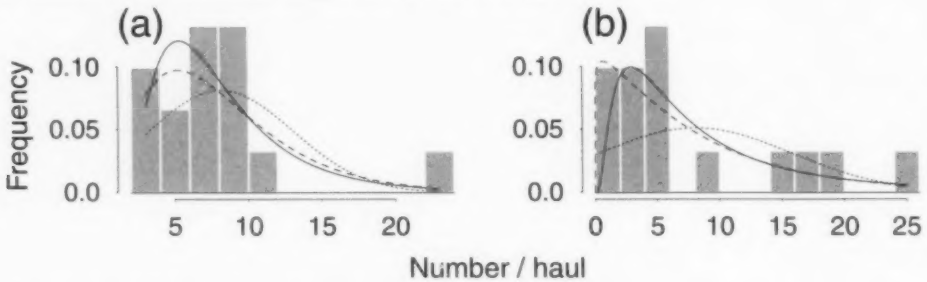
Table 3. Sources of information used for estimating population and community indicators and their reference points for the impact of fishing.

Information type	Description	Research vessel surveys	Landings sampling	Discards sampling
$N(t)$, $N_l(t)$	Population abundance indices (total, by species, by length, by year...)	×		
$B(t)$	Biomass (total, by species, by year...)	×		
$\bar{b}(t)$	Average individual weight	×		
k, L_∞	Growth function parameters (von Bertalanffy)	×		
$C(t)$, $C_l(t)$	Catch in numbers (total by species, by length)		×	×
α	Age at maturity	×		
L_{mat}	Length at maturity	×		
L_c	Length at first capture		×	×

Fig. 1. Example empirical distributions of numbers per haul from French Celtic Sea groundfish survey. (*a*) *Merluccius merluccius*, (*b*) *Scyliorhinus canincula*. Fitted distributions: normal (....), gamma (—), lognormal (- - -).



median are similar (which was the case for all species in the Celtic Sea catch data). It was estimated using numbers at length per species (Table 1, eq. 4). The limit reference point for this indicator is based on the same theoretical idea as the limit reference point Z^* for total mortality, although the data used for estimating them are independent.

Change in fishing mortality required to reverse population growth rate (ΔF)

This indicator is derived from a simple two-stage Leslie-type population dynamics model (Table 1, eq. 5; Rochet and Trenkel 2003). It measures ΔF, the change in fishing mortality required to reverse population growth, keeping all other model parameters constant. To account for the uncertainty in the r estimate, the target population growth rate is corrected by the width of the estimated normal confidence interval (CI; target = $0 - 1.96 \times \sqrt{V[\hat{r}]}$ for stationary or increasing populations, target = $0 + 1.96 \times \sqrt{V[\hat{r}]}$ for decreasing populations). A limit reference point for ΔF has been derived empirically (Rochet and Trenkel 2003). It represents the average interannual variation (expressed as percentage coefficient of variation (CV)) in fishing mortality observed in North Sea and Celtic Sea stocks.

Biodiversity index (Δ_l)

The biodiversity index Δ_l is defined as the probability that two individuals randomly chosen from the community will belong to different species (Table 2, eq. 6; Hurlbert 1971). It is estimated using species abundance estimates.

Partial- and k-dominance curves

The k-dominance curve is the cumulative relative abundance of ranked species plotted against their log rank (Table 2, eq. 7; Clarke 1990). For the partial-dominance curve, the relative abundance of a given species is calculated only with respect to species of lower rank (Table 2, eq. 8; Clarke 1990). The shape of the k-dominance curve is dominated by the single most abundant species. In contrast, the partial-dominance curve allows the study of several of the more abundant species.

Species composition

To detect changes in the species composition with time, we calculate Euclidean distances of time-lagged abundance matrices, regress these distances against the square root of the time lag (linear regression), and use the slope of this relationship as an indicator for change (Collins et al. 2000).

Proportion of noncommercial species

The relative importance of noncommercial species in the community is expressed in terms of either abundance or biomass (Table 2, eqs. 9 and 10). In this study, noncommercial species are all species with no market value. Under the impact of fishing, this proportion is expected to increase. The relationship of the proportion of noncommercial species with time is modelled by a logistic regression (general linear model (GLM) with binomial distribution and logit-link function) where time is the explanatory variable. A positive slope is taken to suggest a significant impact of fishing.

Distribution of mean population length

Using mean length of all individual populations, the distribution of mean length in the community is obtained. Fishing is expected to shift the distribution to smaller lengths. However, it is not obvious how to define the size of a fish, as they continue to grow throughout their whole life. Rather than using L_∞, which is generally poorly estimated for exploited fish populations because of truncated age distribu-

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tions, we use mean length of mature fish to reduce the undue influence of recruits on the estimate. Changes in the distribution of mean population length are detected using a nonparametric Kolmogorov–Smirnov test. The use of this test is justified by the fact that for the species making up the community, for each year a random sampling procedure is used to obtain estimates of mean length by species. Considering mean lengths at the community level means that individual population lengths can change without a change in the community distribution; it is the community distribution that is of interest here.

Size–abundance relationship

The relationship between mean population length and population abundance is supposed to be linear with a negative slope. The reduction in abundance caused by fishing is expected to be higher for species with larger body size, and hence, the slope of the relationship should decrease under the impact of fishing (Table 2, eq. 11; see review in Rochet and Trenkel 2003).

Total biomass and total numbers

These are estimated as the sum of all species biomasses or abundances (Table 2, eq. 12). The effect of fishing on these indicators is unknown, but any increasing or decreasing time trend could be a sign for changes occurring in the community. Hence, a time trend is tested for by means of robust linear regression (MM estimator, which is a maximum likelihood-like estimation method; Franke et al. 1984), which avoids normality assumptions.

Proportion of piscivores

All species in the community are assigned to relevant trophic groups (planktivores, piscivores, and benthivores) on the basis of established knowledge from the literature. The proportion of piscivores (Table 2, eq. 13) is expected to decrease under the impact of fishing as piscivores are the preferred targets of commercial fishing most of the time. Time trends are estimated using logistic regression.

Average individual weight

The average weight $\bar{b}$ of an individual in the community is estimated using total biomass and total abundances (Table 2, eq. 14). It is expected to decrease as the result of fishing as both bigger individuals and larger species are being removed.

Size spectrum

A linear model is used to describe the size spectrum (Rochet and Trenkel 2003; Table 2, eq. 15). Model parameters are estimated using abundance estimates at length (5-cm length classes, all species confounded) and a GLM with log-link and gamma error distribution. Log-transformed lengths, log (L_i), are centred to avoid correlations between parameter estimates. Year effects for both model parameters are tested by comparing model fits with and without year effects using log-likelihood ratio tests (McCullagh and Nelder 1989). The 5-cm length classes were used as a compromise between the desired precision of abundance estimates and the number of length classes available to fit the relationship.

Sampling distributions

For population indicators, sampling distributions and methods used for carrying out hypothesis tests are provided (Table 1, columns 8 and 9). Given the estimation procedures described above, normal distributions are justified for all indicators of this class.

For community indicators, methods used for obtaining sampling distributions, null hypotheses, and alternative hypotheses are summarized (Table 2, columns 4–7). Note that no reference points are available for this class of indicators. Given the estimation procedure, normal distribution assumptions are justified for some indicators. For other indicators, independent parametric bootstraps of species abundance (or biomass) estimates are used and CIs for indicator estimates are obtained using the percentile method. This assumes that species abundance estimates are independent, which seems reasonable for trawl data. For the Celtic Sea example, both lognormal and gamma distributions seem appropriate. Hence, both are used to test the robustness of hypothesis tests to parametric assumptions underlying the implemented bootstrap method. CIs for k- and partial-dominance curves are obtained by recalculating the curves for each bootstrap sample. For testing differences between years, we use pointwise (rankwise) CIs because the comparison tests are for each rank and not for the overall curves. Instead of using parametric bootstraps of individual abundance estimates, we could also have bootstrapped individual hauls (nonparametric bootstrap) and recalculated abundance estimates and indices for each bootstrap sample. Unfortunately, not enough hauls were carried out in some strata for this to be an option for the Celtic Sea survey data.

Power functions

The statistical power of a hypothesis test is the probability that the null hypothesis is rejected given that it is false. A clear description of the concept of power analysis can be found in Peterman (1990). Hence, to calculate the power, it is necessary to know the parametric distribution of the indicator under the alternative hypothesis. Unfortunately, we know the distribution of the alternative hypothesis only for the selected population indicators. As all population indicator estimates are assumed to follow normal distributions, the power function is only described for population growth rate r and total mortality Z. Throughout this study, we will consider an achieved power of at least 0.8 to be satisfactory and use a significance level of $\alpha = 0.05$.

For the intrinsic population growth rate r, the two-sided hypothesis test with H_0: $r = 0$ versus H_1: $r \neq 0$ gives the power function $\beta(r) = 2P_r(G > c - r/\sqrt{V[r]})$, where G is a Student's random variable and $\beta(0) = \alpha$ if $P_r(G > c) = \alpha = 0.025$. The Student's distribution is used because the variance of the slope estimate is unknown and has to be estimated. Given the fitted linearised population model, we calculate the power of the test for detecting an actual growth rate of $r = -0.1$ and hence estimate $\beta(-0.1)$ for all species. Thus we consider that it would be important to detect if a population was decreasing at a rate of –0.1 or more. In the case in which the slope estimation variance is derived from the variance of abundance estimates (see Appendix A) and therefore considered known, G is a standard normal random variable.

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Table 4. Estimated indicators, hypothesis test results, and testing power for detecting indicated values for Celtic Sea groundfish populations.

Species	r	Std(r)	Power $r = -0.1$	$\bar{Z}$	Std($\bar{Z}$)	Power	Z^*	$F/\bar{Z}$	Std($F/\bar{Z}$)
Null hypothesis	$r = 0$		$Z < Z^*$					$F/Z < 0.5$	
Argentina silus	–0.98*	0.23	0.06	1.74**	0.42	0.92	0.4	0.003	0.005
A. sphyraena	–0.9*	0.18	0.06	2.5	0.22	0.50	2.59	0.001	0.001
Arnoglossus imperialis	0.04	0.16	0.07	0.74	0.08	0.50	0.86	0.16	0.09
A. laterna	–0.08	0.33	0.06	1.75	0.36	0.50	2.63	0.008	0.01
Aspitrigla cuculus	–0.06	0.07	0.11	0.75	0.17	0.27	0.56	0.61	0.42
Callionymus lyra	0.17	0.12	0.08	0.02	0.06	NA	$L_c < L_{mat}$	2.06	6.62
Capros aper	0.31*	0.06	0.12	3.01	0.29	#	#	0.01	0.01
Eutrigla gurnardus	0.26	0.43	0.06	0.84	0.21	0.50	1.57	1.66	1.39
Gadus morhua	0.16	0.16	0.07	0.13	0.07	0.50	0.56	11.74	10.2
Hippoglossoides platessoides	0.36	0.31	0.06	2.45**	0.22	1.00	0.53	0.02	0.02
Lepidorhombus whiffigonis	–0.04	0.05	0.16	0.26	0.03	0.50	0.32	2.03*	0.91
Limanda limanda	0.12	0.11	0.08	1.99**	0.4	0.97	0.49	0.17	0.20
Lophius budegassa	0.08	0.03	0.34	0.08	0.06	0.50	0.2	14.11	14.6
L. piscatorius	0.07	0.09	0.08	0.12	0.05	0.50	0.51	5.55	3.65
Merlangius merlangus	0.26	0.28	0.06	0.95	0.11	0.50	2.23	0.25	0.19
Merluccius merluccius	–0.15	0.29	0.06	0.73	1.19	0.12	0.16	0.13	0.23
Micromesistius poutassou	–0.19	0.36	0.06	1.22**	0.13	1.00	0.35	2.0×10^{-4}	0
Nephrops norvegicus	0.41*	0.06	0.12	0.34	0.04	0.50	0.7	14.18	19.47
Pleuronectes platessa	–0.48	0.37	0.06	0.09	0.06	0.50	0.33	5.38	6.82
Scomber scombrus	1	0.65	0.05	0.65**	0.08	0.99	0.3	0.27	0.38
Scyliorhinus canicula	–0.04	0.2	0.06	0.33**	0.05	1.00	0.11	0.25	0.13
Solea vulgaris	–0.04	0.39	0.06	0.01	0.06	NA	$L_c < L_{mat}$	7.97	48.22
Trachurus trachurus	–0.18	0.23	0.06	0.85	0.12	0.50	1.05	0.01	0.009
Trisopterus esmarkii	0.3	0.2	0.06	0.49	0.05	NA	$L_c < L_{mat}$	0.01	0.01
T. minutus	–0.09	0.1	0.08	3.97	0.26	NA	$L_c < L_{mat}$	0.004	0.003

Note: e_F, elasticities of λ to F; Δr, change in intrinsic population growth rate required to significantly invert the population trend; $\Delta F\%$, corresponding point. NA, not available.

[a]ICES (1999*a*, 1999*b*, 2000*b*, 2001).

[b]See Appendix B for source.

For the total mortality Z, the power function for the one-sided hypothesis test H_0: $Z \leq Z^*$ versus H_1: $Z > Z^*$ is $\beta(Z) = P_Z(G > c + (Z^* - Z)/\sqrt{V[Z]})$, where G is again a Student's random variable with number of length classes minus two degrees of freedom, we calculate $\beta(\bar{Z})$, which is the power function of the average of the annual total mortality estimates. A normal random variable is used if $V[\hat{\bar{Z}}]$ is known. The constant c is chosen such that $\beta(Z^*) = \alpha$ if $P_{Z^*}(G > c) = \alpha = 0.05$. Note that we assume Z^* to be known with zero variance.

The variances used in the power functions for given indicator values are those estimated from the fitted models. However, to estimate the increase in power obtainable by increasing the precision of the input information (CV or variance of abundance estimates), the variance of indicator estimates has to be formulated as a function of the CV (or variance) of the input information. This implies that the estimation models are correct. Thus in the case of the intrinsic growth rate r, the linear model has to provide an adequate fit to the log-transformed abundance estimates for this assumption to hold. We have developed the input-dependent variance functions for r and Z (Appendix A). For the remaining population indicators, it is not obvious to us how to obtain these functions.

Before using these variance estimators, it is necessary to verify that they provide similar answers to the model-derived variance estimates. For the intrinsic population growth rate and the total mortality rate, we therefore compare linear model based residual variance estimates with those derived from the variances of abundance estimates (Appendix A) and only use the abundance-based estimator if the latter estimates represent at least 40% of the residual variance. For the total mortality rate, the comparison is carried out for the estimated variance from the GLM model and the variance derived from the abundance estimates (Appendix A).

Celtic Sea groundfish community

The Celtic Sea is a continental shelf sea situated in the triangle between France, Ireland, and Great Britain. The area considered in this study extends from 48 to 51°N and from 6 to 11°W. It supports an international fishery and the main commercial species are assessed by International Council for the Exploration of the Sea (ICES) working groups. Total international landings have increased steadily since the 1950s from ~70 000 t to ~300 000 t in the late 1990s (Pinnegar et al. 2002).

Fisheries information

The French trawler fleet accounts for about one-half of total international landings from this area (estimated from Stock Assessment Working Group Reports). Discard sampling surveys of the French trawler fleet operating in the Celtic Sea

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Power	F/Z from VPA[a]	L_{bar}	Std(l_{bar})	Power	L_{mat}[b]	e_F	e_F from VPA[a]	Δr	$\Delta F\%$	Number of significant tests
		$L_{bar} > L_{mat}$						$\Delta F\% < 20\%$		
0		25.2**	5.4×10^{-3}	1	27.82	–0.0009		0.53	–100	3
0		17.7	2.4×10^{-3}	0	16.83	–0.0003		0.55	–100	1
0		13.0	2.2×10^{-3}	0	12.32	–0.0209		–0.35		0
0		14.3	8.4×10^{-3}	0	11	–0.001		–0.56		0
0.08		19.8**	9.0×10^{-4}	1	25	–0.1346		–0.07		1
0.08		22.4	5.5×10^{-3}	0	17	–0.0241		–0.40		0
0		10.2 #	2.2×10^{-4}	NA	NA	NA		–0.19		1
0.21		22.1**	1.1×10^{-3}	1	24	–0.1394		–1.09		1
0.29	0.83	47.6**	1.1×10^{-2}	1	59	–0.7054	–0.14	–0.48		1
0		17.1**	3.8×10^{-3}	1	20.41	–0.0009		–0.96		2
0.51	0.62	25.7**	2.2×10^{-3}	1	28	–0.2714	–0.09	–0.05		2
0		18.8**	3.6×10^{-3}	1	29	–0.0123		–0.33		2
0.24	0.67	33.1**	1.1×10^{-2}	1	48.05	–0.4905	–0.05	–0.14		1
0.4	0.69	44.6	2.0×10^{-2}	0	35	–0.273	–0.07	–0.25		0
0.002	0.73	30.2	7.3×10^{-4}	0	28	–0.0199	–0.14	–0.41		0
0.001	0.64	23.2**	4.3×10^{-3}	1	50	–0.0296	–0.10	–0.81		1
0	0.64	19.2**	2.6×10^{-3}	1	22.50	0	–0.09	–0.52		2
0.17	0.69	28.3**	5.9×10^{-4}	1	31	–0.8195	–0.09	–0.29		2
0.18	0.84	27.9**	5.8×10^{-3}	1	30	1.8123	–0.12	–0.25	–13	1
0.01	0.63	26.5**	2.6×10^{-3}	1	30	–0.0129	–0.09	–2.29		2
0		44.3**	1.1×10^{-2}	1	54	–0.0271		–0.35		2
0.07	0.85	30.3	1.4×10^{-2}	0	29	–0.0944	–0.12	–0.73		0
0	0.67	23.5**	1.6×10^{-3}	1	24	–0.0012	–0.08	–0.27		1
0		15.8	1.3×10^{-3}	0	14	–0.001		–0.70		0
0		17.1	7.8×10^{-4}	0	13	–0.0002		–0.11		0

percent change in fishing mortality. Hypothesis test results: *, 5% level; **, 1% level; #, test not possible because of lack of information for reference

are undertaken at irregular intervals; the most recent survey was carried out in 1997 (Rochet et al. 2002). French commercial landing information for 1997 was used.

Survey information

In this study we use data from the French groundfish surveys for the years 1997–2000. The survey series, which actually started in 1990, was interrupted from 1992 to 1996 and the survey area was extended in 1997. This change coincided with a change in survey vessel and sampling design. Whereas hauls were placed on a systematic grid for the old design, the new design has stratified random hauls (10 strata). In the year of the change of vessel, an intercalibration study was carried out (Pelletier 1998). Unfortunately, a number of indicators showed important differences between 1990–1991 and the latter part of the series but it proved impossible to disentangle the effects resulting from changes in the survey protocol and changes caused by fishing or other causes. Hence we resolved to remove the first part of the series.

During each cruise, 56 to 69 30-min tows (4 knots) were carried out with a GOV36/47 bottom trawl fitted with a 20 mm mesh codend liner. All fish were identified, weighed by species, and individually measured. The survey trawl is particularly suited for demersal species but not very good at catching benthic species such as megrim (*Lepidorhombus whiffigonis*), anglerfish (*Lophius budegassa*), or *Nephrops*.

Species selection

Abundance indices for many rare or badly sampled species were too unreliable to be used. As a consequence, indicators were not calculated for all species. To select a group of representative species from the studied community, we checked that the size spectrum and the k-dominance curves for selected species were not significantly different from those of the whole community. In this way, a list of 25 species was obtained (see Appendix B). The selected species contributed 99% of the total estimated biomass and around 93% of total estimated numbers. The selected species assemblage contained 17 commercial and eight noncommercial species. They belonged to four trophic groups: demersal benthivores (10 species), demersal piscivores (nine species), pelagic planktivores (four species), and pelagic piscivores (two species). Trophic classifications were based on Whitehead et al. (1986) and Greenstreet (1996).

Results

Case study

Growth rate estimates for 21 populations indicated that there was no evidence to reject the null hypothesis of a zero growth rate, whereas two populations were significantly increasing (boarfish (*Capros aper*) and Norway lobster (*Nephrops norvegicus*)) and the two Argentine species were significantly decreasing (Table 4). Note that one of the de-

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creasing populations is a noncommercial species. The power to detect actual intrinsic growth rates of –0.1 was below 0.1 for most species (Table 4). The power of tests when varying the precision of input abundance estimates were calculated for those species for which the error variance based on abundance estimates was at least 40% of the residual model variance to use the approximation given in Appendix A (Fig. 2). Among the selected species, the achieved power was highest for black angler (*Lophius budegassa*). For dab (*Limanda limanda*), in contrast, the precision of estimated abundance indices would need to be multiplied by about 4 (CV divided by 4) to detect a growth rate of around 0.31 (estimated growth rate 0.12) being significantly different from zero with a power of 0.8.

Total mortality estimates Z were obtained by assuming stable population length structures in any given year (Table 4). The results confirmed that for 17 populations, length structures were indeed stable as estimates were not significantly different between years (two-sided 5% level tests; results not shown). Nevertheless, average (over all years) total mortality estimates were calculated for all species, and one-sided tests (2.5% significance level) revealed that for six species, total mortality was outside safe limits ($Z > Z^*$); the test could not be carried out for one species (*Capros aper*) because of the lack of information necessary to calculate the limit reference value Z^*. For four species, Z^* was negative because L_c was smaller than L_{mat}, which implies that whatever the value of Z, it cannot be too high. Thus overall, for 18 species, no evidence was found to reject the hypothesis of acceptable levels of total mortalities, given the high uncertainties inherent in mortality estimates and ignoring any uncertainty in the estimates of Z^*. Total mortality estimates for selected species using every year of the time series separately show that estimates are rather similar between years except for *Limanda limanda* and perhaps *Scomber scombrus*, where estimates varied somewhat between years, indicating that the population length structure might not be stable (Fig. 3). Statistical powers were calculated using the mean of the annual estimates. They were around one for most species but there were notable exceptions with very low power. For *Scomber scombrus*, the variance of the total mortality estimate (for the year 1998) derived from the variance of the input abundance estimates was only 57% of the estimated variance from the GLM model. Hence the calculated power of the hypothesis test for different CVs of abundance estimates is only an indication of the kind of increase in power obtainable by reducing the CV of abundance estimates (Fig. 3).

Looking at F/Z, the estimated value was found to be significantly above the limit reference point of 0.5 (one-sided 5% level) for only one species. For a number of species, the nonsignificant results were due to unsatisfactory testing powers as a result of low estimation precision. Assuming catchabilities equal to 1 when estimating abundance indices certainly led us to underestimate certain population abundances. Thus we overestimated F and as a consequence obtained large F/Z estimates. Support for this explanation comes from the comparison of our F estimates with those obtained by the ICES Stock Assessment Working Groups (ICES 1999*a*, 1999*b*, 2001). The resulting exploitation rates are generally much lower than ours, although the opposite case occurred for hake (*Merluccius merluccius*), whiting (*Merlangius merlangus*), blue whiting (*Micromesistius poutassou*), mackerel (*Scomber scombrus*), and horse mackerel (*Trachurus trachurus*) (Table 4).

The test for the impact of fishing on population length structure is based on the comparison of L_{bar} with L_{mat}. This test was found to be less optimistic because no evidence was found for only 10 populations that were not in the safe range ($L_{bar} > L_{mat}$). For 15 populations, L_{bar} was significantly lower than L_{mat} with statistical powers of one (Table 4).

Large reductions (100%) in fishing mortality would be required to significantly invert the decreasing population trends of the two populations with r significantly smaller than zero (Table 4). Thus the estimated necessary changes in F are much higher than the suggested 20% limit reference point because high uncertainty in r estimates led to large target changes. For all other populations, negative elasticities combined with negative large target changes in r yield unreliably high estimated increases in fishing mortality required to make the populations decrease. The only exception is plaice (*Pleuronectes platessa*), which has an unexpectedly positive elasticity of population growth rate to fishing mortality because estimated r was higher than Z. These inconsistent estimates probably arise from various errors and uncertainties in the data, as indicated by the large variance estimates.

We now turn to test results for community indicators. There was no significant linear trend in biodiversity as measured by Δ_1 (Fig. 4; Table 5). CIs based on gamma and lognormal parametric bootstraps were similar. Likewise, neither k-dominance curves nor partial-dominance curves changed their form significantly over time (Fig. 5). CIs based on gamma and lognormal parametric bootstraps were similar (results not shown). Despite their stable form, an inversion in the dominant species was observed. Blue whiting was the most abundant species in 1997, but boarfish was most abundant in 2000. The shape of k-dominance curves was entirely determined by the four most abundant species. Compared with k-dominance curves, partial-dominance curves suggested a more even community structure. No consistent changes with time were found for the species composition (Table 5); the estimated slope of Euclidean distances of time-lagged abundance matrices regressed against the square root of the time lag was 1.3×10^9 (2.5 and 97.5 percentiles: -4.1×10^9 and 4.9×10^9).

The distribution of mean population lengths (survey) fluctuated from year to year (Fig. 6). However, no significant change was detected in the distribution when comparing 1997 with 2000 (Table 5). No significant linear relationship between mean size and population abundance index was found for any of the study years, hence we could not test for changes in the relationship. However, scatterplots were similar between years, with most species remaining in the same position, indicating that whatever the relationship form, it was rather stable over the study period (Fig. 7).

The proportion of noncommercial species (no commercial value) in biomass in the community remained rather stable over the study period (Table 5), whereas the proportion in numbers increased significantly from [0.20, 0.38] in 1997 to [0.47, 0.70] in 2000; the ranges are 95% CIs based on a parametric bootstrap (gamma distribution). The increase in the proportion of noncommercial species in numbers was

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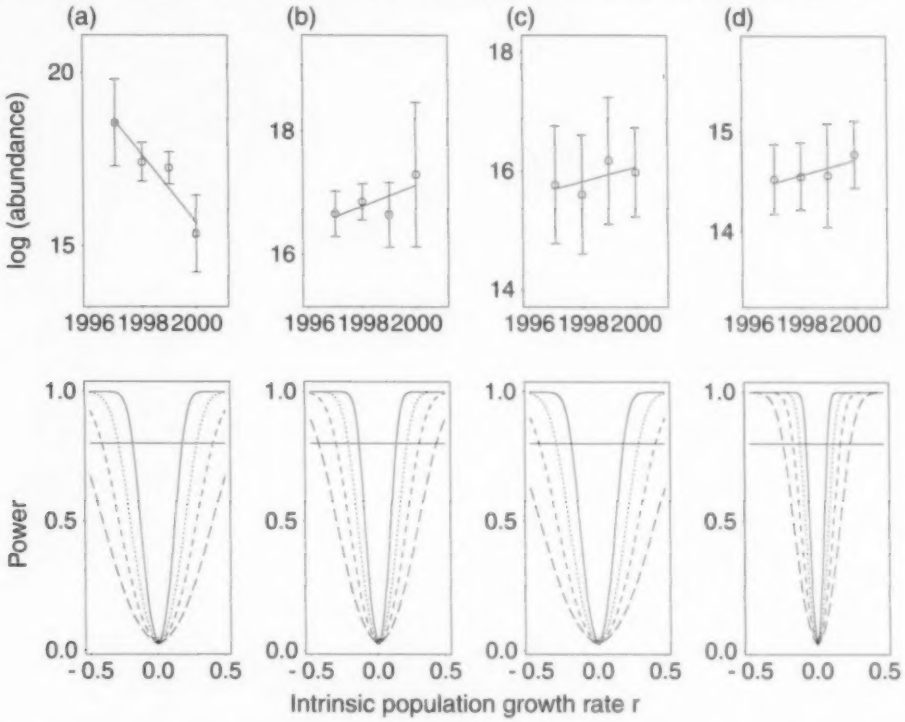
Fig. 2. Abundance estimates (top row) and intrinsic population growth rate and estimates of power of hypothesis test (bottom row; observed CV/10 (—), observed CV/4 (....), observed CV/2 (- - -), observed CV (– – –)). For H_1: $r < -0.1$, for selected species of Celtic Sea groundfish community: (*a*) *Argentina silus*, (*b*) *Callionymus lyra*, (*c*) *Limanda limanda*, (*d*) *Lophius budegassa*.



mainly due to a (significant) increase in boarfish and a (nonsignificant) increase in poor cod (*Trisopterus esmarkii*). As boarfish is the second most abundant species and has a rather small body size (maximum body length of around 20 cm), it contributed to the increase in noncommercial numbers but not biomass.

No time trend in either total biomass or total abundance of animals in the community was found, although there was a slight nonsignificant decreasing trend of mean weight of individuals in the community. The proportion of piscivores expressed as biomass or as numbers did not show a significant time trend over the study period (Table 5).

No significant differences between years were found for the slope of the size spectra; however, the size spectra were shifted vertically (Table 5). A model with separate intercepts for each year provided a significantly better fit compared with a model with a common intercept (example in Fig. 8). No improvement in fit was found when including year effects for the slope parameter. As there was no time trend in estimated annual intercepts, we concluded that no directed change occurred in the size structure of the community. Changes in the intercept followed variations in total abundance and biomass, as the intercept of the size spectrum is clearly an index of community abundance–biomass.

Indicator performance

The performance of indicators was evaluated using three criteria: the achieved precision of the indicator estimate expressed as percentage CV, the power of the hypothesis tests (when available), and the existence and justification of the reference point (Table 6). In terms of precision, L_{bar} of individual species was most precise with an average CV of 0.02%; r and F/Z were least precise, with CVs of around 100%. Most other indicators had reasonable CVs of around 20%.

In terms of testing power, L_{bar} came first again, with satisfactory power for 15 of the 25 species tested. This test was only carried out for 1 year (1997), because it requires discard estimates, which were not available for all years. Testing powers were similar for total mortality estimates but low for the intrinsic population growth rate. Test powers could not be calculated for any of the community indicators.

Target or limit reference points are only available for the population indicators, whereas the expected direction of change is known for some community indicators. The biodiversity index as well as the slope of the size spectrum can be estimated rather precisely. Because of the lack of reference points, absolute values or changes in values give no indication as to the importance of the impact of fishing.

Discussion

Case study

Overall, not much evidence was found for rejecting the general null hypothesis that no change had happened to the structure of the Celtic Sea groundfish community during the study period. However, many ongoing changes might have remained undetected because of the shortness of the time

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Fig. 3. Annual total mortality rate estimates based on equilibrium assumption for selected species of Celtic Sea groundfish community (test value Z^* horizontal lines): (*a*) *Argentina silus*, (*b*) *Callionymus lyra*, (*c*) *Limanda limanda*, (*d*) *Lophius budegassa*, (*e*) *Scomber scombrus*. (*f*) Example of statistical power of hypothesis test H_0: $Z < Z^*$ for *S. scombrus* for different values of variance of input abundance estimates using the coefficient of variation (CV) derived from the observed variance of abundance estimates in 1997 (– – –), observed CV/10 (—), CV/4 (....), and CV/2 (- - -). Point estimate for total mortality using 1997 data (solid horizontal line) and limit reference point Z^* (dotted vertical line).

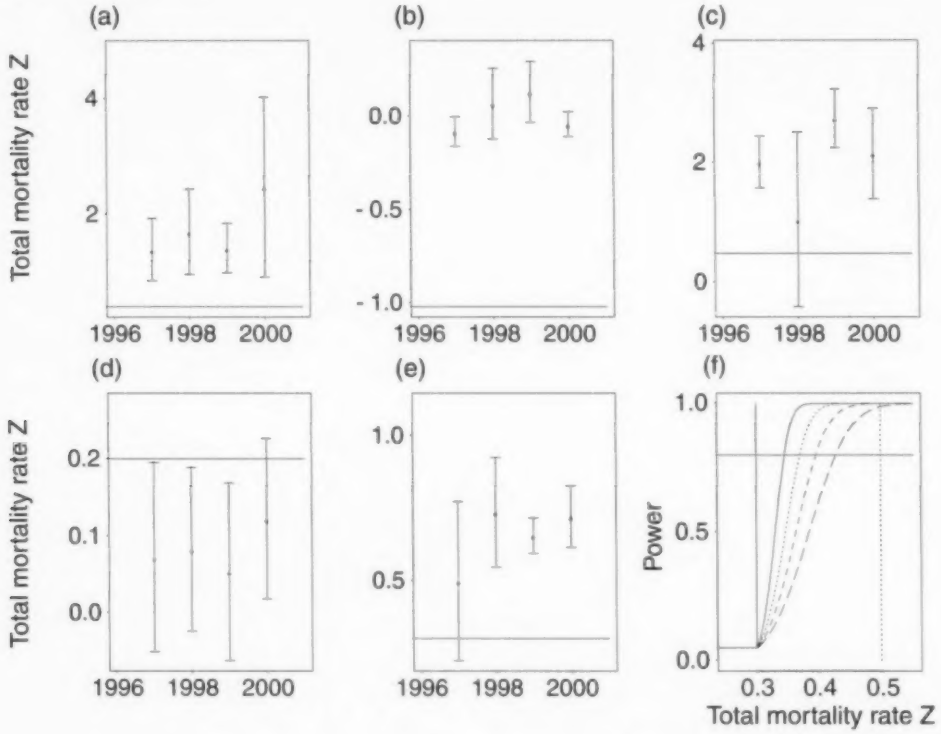
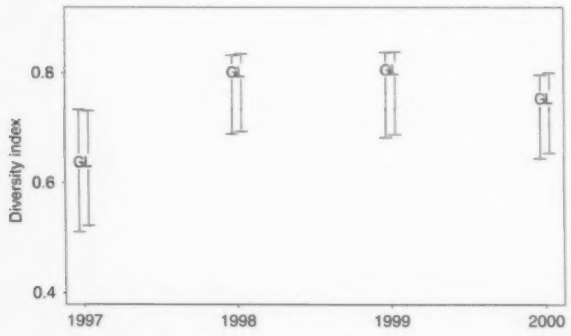


Fig. 4. Diversity index Δ_1 (probability of interspecies encounters) with 95% confidence intervals for Celtic Sea groundfish community (G, gamma parametric bootstrap; L, lognormal parametric bootstrap).



series and imprecise estimates that resulted in low statistical power of some tests. On the other hand, as the Celtic Sea has been increasingly exploited during the last 30 years, changes might have happened long before the period considered in this study.

When considering populations individually, we saw that fishing was an unimportant source of mortality for noncommercial species. However, because of the high uncertainty in some indicator estimates, statistical power varied largely. Uncertainty was also responsible for the failure as an indicator of the change in fishing mortality required to reverse a population trend.

We use the number of significant hypothesis tests for each species to identify apparently impacted species. The most impacted species was *Argentina silus*, a commercial pelagic planktivore. The population was found to decrease significantly ($\hat{r} = -0.98$) and had far too high total mortalities ($\hat{Z} = 1.74 > Z^* = 0.4$) and L_{bar} below L_{mat} ($L_{bar} = 25.2 < L_{mat} = 27.82$). Judging from the very low exploitation rate estimate ($\hat{F}/\hat{Z} = 0.003$), the very high natural mortality rate is not caused by fishing. This seems unlikely and casts some doubt on the exploitation rate estimate, a doubt raised before (see Results). All second most impacted species are commercially exploited, with the exception of long rough dab (*Hippoglossoides platessoides*), and belong to various trophic groups. Hence, feeding type does not provide an explanation for the findings, which is confirmed by the stable proportion of piscivores. For long rough dab, the significant hypothesis tests of both total mortality and L_{bar} indicate that the population is impacted and thus would be expected to decrease.

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Table 5. Hypothesis test results for community indicators for the Celtic Sea groundfish community.

Indicator	Test result	Significance test
Biodiversity Δ_1	No change over time	N
k-dominance curve	No change in shape over time	N
Partial-dominance curve	No change in shape over time	N
Species composition	No change in composition over time	N
Proportion of noncommercial species[a]	Increase in numbers, $p = 0.002$	Y
	No increase in biomass, $p = 0.13$	N
Distribution of mean length in community	No difference between 1997 and 2000 ($p = 0.9995$)	N
Size–abundance relationship	No linear relationships found; no test possible	NA
Total biomass	No linear time trend, $p = 0.85$	N
Total numbers	No linear time trend, $p = 0.93$	N
Proportion of piscivores	No decrease in numbers, $p = 0.58$	N
	No decrease in biomass, $p = 0.17$	
Average individual weight in community	No linear trend, $p = 0.712$	N
Shape of size spectrum	Year effect for intercept, $p = 0.04$	N
	No year effect for shape parameters, $p = 0.845$	

Note: All tests are carried out with 5% significance levels. NA, not available.
[a]For names of noncommercial species, see Appendix B.

However, a positive intrinsic growth rate was estimated, though the estimation precision was low. Similar results were found for dab and mackerel. In contrast, for two species (*Micromesistius poutassou* and *Scyliorhinus canicula*), negative growth rate estimates occurred in conjunction with significantly high total mortality estimates and high L_{bar}. In general, significantly large L_{bar} were found to occur for both increasing ($r > 0$) and decreasing ($r < 0$) populations. In only five of 15 significant cases were $\hat{L}_{bar}$ estimates at least 5 cm larger than L_{mat}. Given that L_{mat} are also estimated and that this uncertainty was not taken into account, it seems that the hypothesis tests for $\hat{L}_{bar}$ were too sensitive. Thus, uncertainty in the limit reference points should be taken into account; this applies to $\hat{L}_{mat}$ as well as to $\hat{Z}^*$.

Community indicators should add another point of view to the diagnostic obtained from looking at single populations. However, few detectable changes were found in community structure. The only indicator pointing at changes was the proportion of noncommercial species, which increased. The individual population analysis had already revealed this for *Capros aper*.

Generally speaking, our aim to obtain clear answers was hindered by large uncertainties in survey abundance estimates as well as biased abundance estimates resulting from a lack of catchability estimates. In particular, estimates of fishing mortality seemed to be too high in comparison with estimates obtained by virtual population analysis (VPA). Coefficients of variation for indicator estimates varied between 1 and 200%. In comparison, abundance, biomass, and discard estimates had CVs of 30–40%. For certain indicators, this large uncertainty prevented us from drawing firm conclusions. This was particularly true for the intrinsic growth rates, which were estimated with low precision. To prove intrinsic population growth rates of around 0.1 to be significantly different from zero, for most species, the CV of abundance estimates would need to be at least divided by four from the achieved 30% to something around 8%. This would imply a large increase in the number of hauls per survey. Even so, the required precision might not be achievable because of the nonrandom spatial distribution of many species and environment-driven interannual variations.

Despite the uncertainties, the emerging picture is that fishing impacted a number of populations of the Celtic Sea groundfish community primarily because individuals of too small a size were killed. This might be caused by too small mesh sizes used by bottom trawlers. This conclusion is supported by the large amounts of small fish discarded by the French bottom trawlers (Rochet et al. 2002). The impacted species were almost exclusively commercial species. As a result and because of the increase of one noncommercial species, the overall proportion of noncommercial species rose over the study period.

Indicator performance

The performance of indicators was evaluated using the achieved precision of the indicator estimate expressed as percentage CV, the power of the hypothesis tests (when available), and the existence and justification of the reference point. L_{bar} of individual species was most precisely estimated and hence scored best in terms of testing power.

Most reference points for population indicators are estimates with unknown precision. In the case of L_{bar} and Z, theory exists to motivate the choice, although the actual value has to be estimated. We used published biological parameters with unknown precision for the estimation, which precluded us from estimating the precision of reference points. Were this information available, hypothesis tests could easily be adapted. The reference point for the exploitation rate is clearly the most arbitrary. Currently no reference points are available for any of the community indicators. Nevertheless, for some community indicators it is possible to ascertain the expected direction of change. Hence these indicators are preferable to those for which not even the direction of change is known.

In this study we tested the new indicator ΔF, which describes the change in fishing mortality required to reverse

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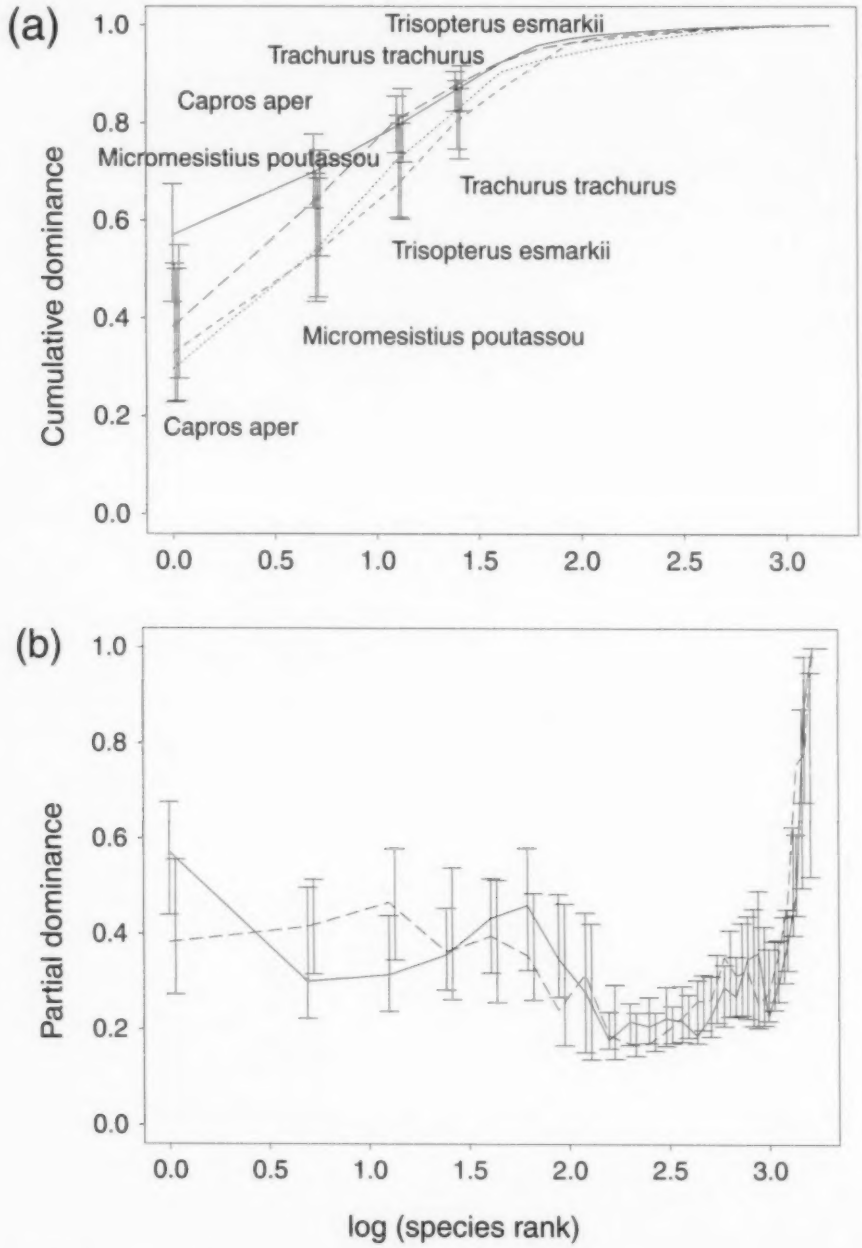
Fig. 5. Annual *k*-dominance curves (*a*) and partial-dominance curves (*b*) for Celtic Sea groundfish community with pointwise 95% confidence intervals (gamma parametric bootstrap). Dominant species are indicated for 1997 and 2000. Lines: 1997 (—), 1998 (.....), 1999 (- - -), and 2000 (– – –).



decreasing population growth. Significantly negative population growth was found for only two populations, as growth estimates were generally imprecise. Under these circumstances very large changes in fishing mortality would be necessary to reverse population growth. Unfortunately, the approximations used for carrying out the calculations are not applicable if very large changes in F are necessary. Hence, the results obtained for this indicator have to be taken with care.

Having looked at indicators individually, we now turn to investigate the agreement between population indicators. Some of the indicators are theoretically linked and should therefore provide the same answers. As expected, test results for Z and L_{bar} showed the largest agreement: both tests were significant for six species; nine additional species had significant tests for L_{bar} only. Thus, for the case study, Z did not provide any information that was not provided by L_{bar}. In

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Fig. 6. Distribution of mean population lengths (log-transformed) in Celtic Sea groundfish community based on representative species selection. (*a*) 1997, (*b*) 1998, (*c*) 1999, and (*d*) 2000.

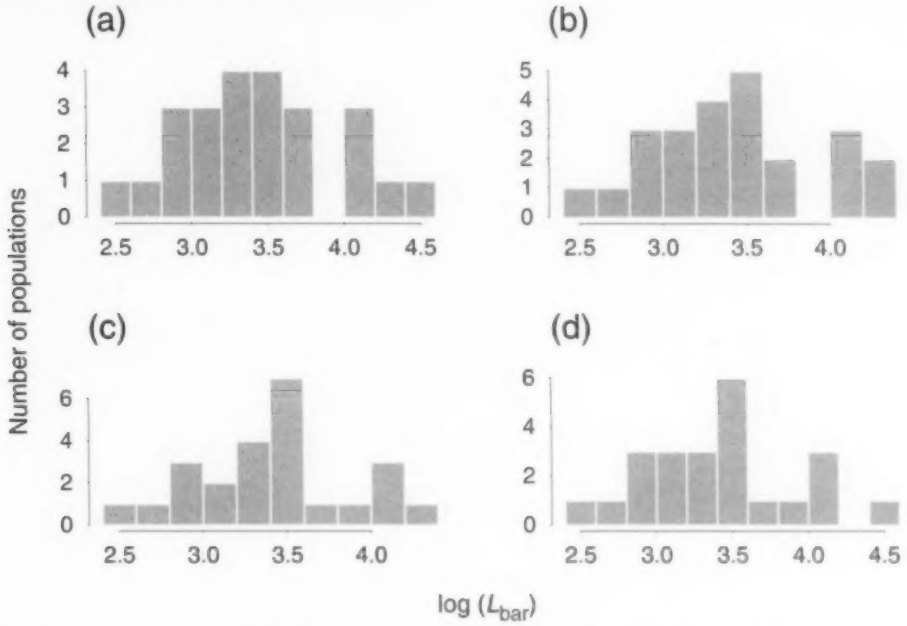
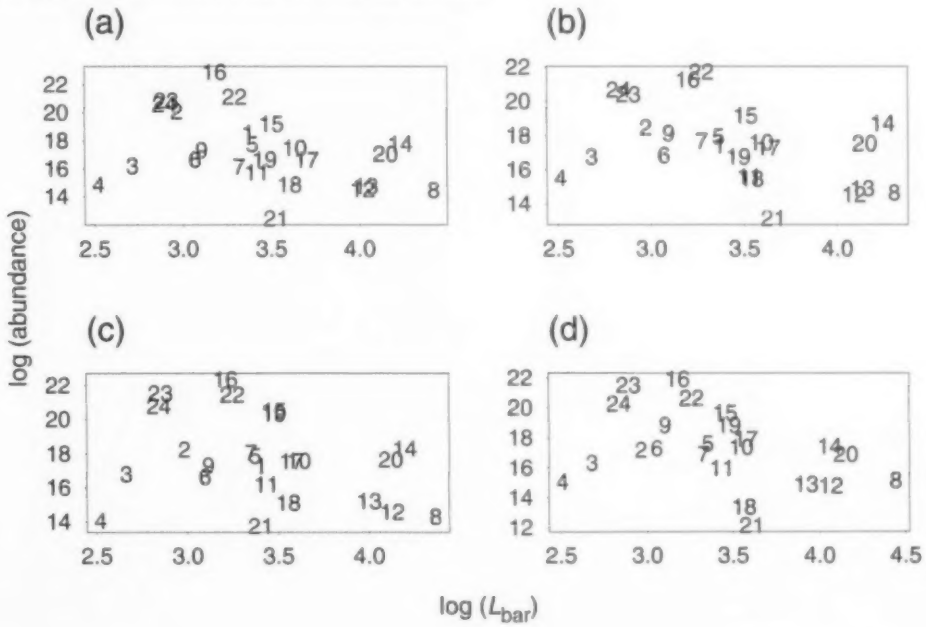


Fig. 7. Annual size–abundance relationship on log scale for Celtic Sea groundfish community based on representative species selection (numbers refer to species): (*a*) 1997, (*b*) 1998, (*c*) 1999, and (*d*) 2000.



addition, the latter was estimated with higher precision and had satisfactory testing power for most species. Unfortunately, the estimation of L_{bar} requires discard as well as landing information and is therefore probably not feasible for many populations. In two cases, null hypotheses were simultaneously rejected for L_{bar} and r, although r was positive in one case and negative in the other.

In conclusion, L_{bar} was found to be a powerful population indicator. As catch data rely on generally expensive discard sampling, we suggest that the merits of alternative length-

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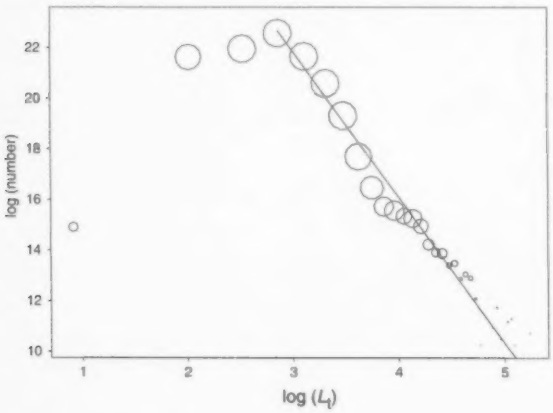
Table 6. Performance and characteristics of indicators for the impact of fishing on the Celtic Sea groundfish community and precision of input information.

Measure	No. of estimates	Precision (% CV) Median	Mean	Power of hypothesis test, no. of tests ≥0.8	Reference point status	Type of indicator
Input information						
$\hat{N}_i(t)$	100	28	34			
$\hat{B}_i(t)$	100	28	33			
$\hat{D}_i(t)$	25	40	46			
$\hat{F}_i(t)$	25	80	92			
Indicator estimates						
L_{mat_i}	25	0.02	0.02	15/25	Unknown precision	Population state
Size spectrum (slope)	4	1	10	NA	NA	Community state
$\hat{\Delta}_1(t)$	4	9	9	NA	NA	Community state
$\hat{Z}_i(t)$	100	12	20	6/20	Unknown precision	Population state
Proportion piscivores (biomass)	4	14	14	NA	Direction	Community state
$\hat{B}(t)$	4	16	15	NA	NA	Community state
$\hat{N}(t)$	4	18	18	NA	NA	Community state
Proportion noncommercial						
Abundance	4	19	18	NA	Direction	Community state
Biomass	4	21	22	NA	Direction	Community state
Proportion piscivores (abundance)	4	22	22	NA	Direction	Community state
$\bar{b}(t)$	4	26	26	NA	Direction	Community state
$\hat{r}_1$	100	106	196	0/25 ($r = -0.1$)	Theoretical basis	Population state
$\hat{F}_i/\bar{\hat{Z}}_i(t)$	25	103	130		Arbitrary	Fishing pressure
$\Delta\hat{F}_i$		NA	NA	NA	Unknown precision	Management response

Note: Indicators are ordered by decreasing precision. NA, not available; D, discards.

Fig. 8. Size spectrum for Celtic Sea groundfish community for 1999 based on all species. Bubble size is proportional to the number of hauls in which the length class was present.



based indicators such as mean or median length in individual populations and possibly in the community should be explored, including the definition of appropriate reference points. For community indicators, only estimation precision and the existence of an expected direction of change could be compared. The biodiversity index Δ_1 and the parameters of the model describing the size spectrum were found to be estimated most precisely. Unfortunately, their expected direction of change is currently not available. In contrast, estimates of all indicators for which this is the case, e.g., average individual weight in the community, the proportion of piscivores, and the proportions of noncommercial species, had CVs of 14–30%.

Input data

Two shortcomings concerning the Celtic Sea data can be identified: unknown catchability factors and imprecise abundance estimates. Regarding catchability, indicators based on proportions are only affected by relative catchability, which we assumed to be equal for all species. In contrast, indicators based on absolute abundance indices additionally suffer from bias resulting from the relationship between indices and population numbers. We think that this was the main cause for our unreliable estimates of fishing mortality. Some confidence that community indicators (e.g., biomass, mean weight, Shannon's index) are robust to the particular survey design and thus variations in catchability come from studies using data obtained with different survey gear (Wantiez 1996). However, this is not true for population indicators.

Imprecise abundance estimates are to a large extent due to the spatial distribution of animals, which for many species is not uniform over the study area for various reasons, including substrate type and depth. Hence the underlying population distributions are skewed, and increasing the number of hauls would increase the precision of abundance estimates but probably only slowly. However, this points to another dimension that needs to be considered when studying indicators for the impact of fishing: the spatial scale. Although the appropriate spatial scale might be the stock area for a single population, it is not obvious what it should be for a community. Some evidence for the importance of the spatial scale is provided by the finding that species diversity is an exponen-

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tial function of the size of offshore banks (Frank and Shackell 2001). On the other hand, it seems obvious that the more homogenous the underlying community is, the more precise indicator estimates are going to be. For the Celtic Sea, we could choose sampling strata as units for the assessment, with the problem, however, that the number of hauls per stratum varies from 2 to 23 depending on strata area (mean = eight hauls), thus causing the problem of variable precision.

Statistical issues

Two main statistical issues arise from this study: multiple testing and parametric assumptions made for obtaining indicator distributions. For population indicators, five hypothesis tests were carried out separately for each population. Multiple testing increases the chances of finding spurious results. Bonferroni-adjusted significance levels were used to look at the tests of all five indicators together. The conclusions remain unchanged from individual tests for the reasonably precise indicators L_{bar} and Z. The question remains of adjusting the testing level of the same indicator across species. We would argue that it is reasonable to consider populations separately and hence not to adjust individual population tests for the same indicator. Indeed, adjustments seem to be required only if the individual population tests serve as evidence for the overall significance of an indicator.

For a number of community indicators we had to resort to parametric bootstraps of the abundance estimates. We found that the results for the Celtic Sea groundfish community were rather insensitive to the chosen parametric distribution. Both gamma and lognormal distributions for abundance estimates led to similar indicator estimates and identical conclusions for hypothesis tests. Thus the results presented seem to be robust to this assumption.

Based on the results presented, we would recommend using L_{bar}, Z, $\bar{b}$, and the proportion of noncommercial species, which can all be estimated with reasonable precision and for which we know what kind of effect fishing has. In addition, size spectra might have some potential provided that theoretical developments or large empirical studies will allow better prediction of the effects of fishing and the setting of reference points. Given that the achievable precision of different indicators varies, when a synthesis of indicator results is attempted, for example, using multivariate methods such as canonical correlation analysis or principal component analysis, indicator results should be weighted appropriately, for example, by the inverse of their precision. The choice of indicators to include in the first place should, however, be guided by their importance with respect to management goals.

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Appendix A

In the standard linear model $Y = \alpha + \beta X$, the estimated slope β (estimated by least squares) follows the normal distribution $\beta \sim N((X'X)^{-1}X'Y, \sigma^2(X'X)^{-1})$. Given that the model is correct, the residual variance is equal to the variance of independent observations and the following estimator applies: $\hat{\sigma}^2 = V[\hat{\varepsilon}]$. In estimating linear time trends of a given indicator, given that it can be assumed to be normally distributed, $\hat{\sigma}^2$ is estimated as the average of the annual variances.

The variance of intrinsic growth rate as a function of the CV of abundance indices is estimated approximately based on standard regression theory as $\hat{V}[\hat{r}_i] = (t't)^{-1} \ln(\mathrm{CV}[\hat{N}_i]^2 + 1)$ with t the centred time vector. This uses the standard result that for lognormal variables the variance of the log-transformed data is approximately given by $V[\ln(N)] \approx \ln(\mathrm{CV}[N]^2 + 1)$. The power function of the hypothesis test for different CV estimates relative to the CV obtained with the actual data can then be calculated.

The variance of total mortality as a function of the variance of the input abundance estimates is obtained using the following approximation based on the log-transformed estimation model (eq. 2 in Table 1):

$$V[\hat{Z}_i] \approx (X_i'X_i)^{-1} \ln\left(\frac{1}{L}\sum_{l=1}^{L}\frac{\sqrt{V[\hat{N}_{i,l}]}}{N_{i,l}} + 1\right)$$

where L is the number of length classes, X_i is a vector with elements

$$x_{l,t} = t_{0_i} - \frac{1}{k_i}\ln\left(1 - \frac{l_l}{L_{\infty_i}}\right)$$

and l_l is the length corresponding to the midpoint of length class l.

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Appendix B

Table B1. Selected species for an assessment of fishing on the Celtic Sea groundfish community.

	Species	Name	α	Source	A_{max}/M	Source	L_{mat} source	L_∞	k	Source	Trophic group[a]
1	*Argentina silus*	Greater Argentine	4–9	B	30–35	B	E	42.7♂	0.21♂	We	PEPA
								48.87♀	0.16♀		
2	*Argentina sphyraena*	Argentine	1.8	F	7	F	E	28.4	0.41	F	PEPA
3	*Arnoglossus imperialis*	Imperial scaldfish	3	F	11	Q	E	20	0.26	F	DEBE
4	*Arnoglossus laterna*	Scaldfish	2–3	G	9	G	F	21.1	0.26	F	DEBE
5	*Aspitrigla cuculus*	Red gurnard	1.4–2	F	20	F	F	43.1	0.31	FT	DEBE
6	*Callionymus lyra*	Dragonet	2.5	J	6	F	F	23	0.51	F	DEBE
7	*Capros aper*	Boar fish						19	0.5	Guess	DEBE
8	*Eutrigla gurnardus*	Grey gurnard	3.5	F	16	F	F	40.5	0.38	FT	DEPI
9	*Gadus morhua*	Cod					F	109.5	0.38		DEPI
10	*Hippoglossoides platessoides*	Long rough dab	2–3	Q	10	Q	F	40	0.28	F	DEBE
11	*Lepidorhombus whiffigonis*	Megrim	2.8	W	0.2	W	F	66	0.11	D	DEPI
12	*Limanda limanda*	Dab	2.6	DT			F	41.8♀	0.54♀	DT	DEBE
								36.1♂	0.63♂		
13	*Lophius budegassa*	Black anglerfish	7	W	0.15	W	E	100	0.11	D	DEPI
14	*Lophius piscatorius*	Monkfish	6	W	0.15	W	F	150	0.088		DEPI
15	*Merlangius merlangus*	Whiting	2	W	0.2	W	F	66.2	0.175	D	DEPI
16	*Merluccius merluccius*	Hake	3.8	W	0.2	W	R	127.5	0.074	D	DEPI
17	*Micromesistius poutassou*	Blue whiting	3.2	W, Q	16–20	Q, F	R	39.9	0.15	D	PEPA
			3–5	F							
18	*Nephrops norvegicus*	Norway lobster			0.3	W	W	68.2♂	0.124♂	D	DEBE
			3.4♀	V, W	0.2			49.2♀	0.17♀		
19	*Pleuronectes platessa*	Plaice	3	W	0.12	W	R	49.8	0.165	D	DEBE
20	*Scomber scombrus*	Mackerel	2	W, Q	6–20	Q, F	F, R	36.2	0.49	D	PEPI
			3.5	F							
21	*Scyliorhinus canicula*	Small-spotted catshark	5	F	22	F	F	90.0	0.09–0.13	R	DEPI
22	*Solea vulgaris*	Sole	3	W	0.1	W	R	33.6♂	0.378♂	D	DEBE
								42.5♀	0.278♀		
23	*Trachurus trachurus*	Horse mackerel	3.5–4.5	W, Q	15	Q	R	44.9	0.2	T	PEPI
24	*Trisopterus esmarkii*	Norway pout	2.3	J	3–8	Q, F	F	23	0.52	J	PEPA
25	*Trisopterus minutus*	Poor cod	1–4	F	5	Q	F	33.5	0.18–0.48	A	DEPI

Note: Published information on their life-history traits. Commercial species are underlined. PEPA, pelagic planktivore; PEPI, pelagic piscivore; DEBE, demersal benthivore; DEPI, demersal piscivore. Sources: A, Albert (1991); B, Bergstad (1993); D, Dorel et al. (IFREMER, 44311 Nantes, France, unpublished data); DT, Deniel and Tassel (1986); E, estimated from age at maturity and growth parameters; FT, Fontaine and Theret (1982); F, FishBase, Froese and Pauly (1999); G, Gibson and Ezzi (1980); J, Jennings et al. (1999); T, Trouvery (1978); Q, Quéro (1984); R, http://www.ifremer.fr/maerha/life_history.html; V, Verdoit (1999); W, ICES Working Groups (ICES 1999*b*, 2001); We, Westhaus (1982).

[a]Whitehead et al. (1986) and Greenstreet (1996).

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PERSPECTIVE

Which community indicators can measure the impact of fishing? A review and proposals

Marie-Joëlle Rochet and Verena M. Trenkel

Abstract: Population and community descriptors that might be used as indicators of the impact of fishing are reviewed. The criteria used for the evaluation of these indicators are meaning, expected effect of fishing, exclusiveness to fishing effects, and measurability. Population indicators such as total mortality rate, exploitation rate, or average length are the most operational indicators because their meaning is clear and the expected effect of fishing on them is well understood so that reference points can be set. On the other hand, indicators based on the composition of species assemblages such as diversity indices and ordination of species abundances are difficult to interpret, and the effect of fishing on them is not easily predicted. Robust indicators describing the community functions of interest (production and transfer of biomass to large fish), such as size spectra descriptors or the proportion of piscivorous fish in the community, are more promising but are not yet well developed. New candidate indicators are proposed: the change in fishing mortality required to reverse population growth rate, the proportion of noncommercial species in the community, and the average length and weight in the community.

Résumé : Cet article passe en revue des descripteurs de population et de communauté qui pourraient être utilisés comme indicateurs de l'impact de la pêche. Les critères utilisés pour l'évaluation de ces indicateurs sont leur signification, leur sensibilité à la pêche, la spécificité de leur réponse à la pêche, et leur mesurabilité. Les indicateurs de population comme le taux de mortalité totale, le taux d'exploitation ou la taille moyenne sont les indicateurs les plus opérationnels car leur sens est clair, l'effet de la pêche sur leurs variations est bien compris et des points de référence peuvent être fixés. En revanche, les indicateurs fondés sur la composition spécifique des assemblages, comme les indices de diversité ou les analyses multivariées des abondances d'espèces, sont difficiles à interpréter et l'effet de la pêche sur eux est imprévisible. Des indicateurs robustes décrivant les fonctions utiles de la communauté (i.e., la production et le transfert de biomasse vers les grands poissons), comme les descripteurs des spectres de taille ou la proportion de poissons piscivores dans la communauté, semblent plus prometteurs mais ils ne sont pas encore au point. De nouveaux indicateurs potentiels sont aussi proposés : le changement de mortalité par pêche nécessaire pour inverser le taux de croissance de la population, la proportion d'espèces non commerciales dans la communauté, et la taille moyenne dans la communauté (en poids ou en longueur).

Introduction

Fisheries science and management are progressively switching their attention from single species to ecosystems (Anonymous 1999; ICES 2000*a*), increasing the need for measuring the impact of fishing on ecosystems. Large efforts are devoted to the construction of indicators for marine capture fisheries at various levels from populations to ecosystems (Caddy and Mahon 1995; Garcia and Staples 2000). As a result, many indicators targeting various components of ecosystems have been developed, and used, based on experience or on more or less explicit assumptions stemming from diverse ecological theories. Now it is time to take stock of what is available, what makes sense, and what is lacking. Indicators useful for fisheries management should be able to measure the impact of fishing and be easy to estimate with commonly available data. This paper critically reviews and classifies indicators of the effects of fishing on fish communities, focusing on their meaning and sensitivity to fishing impacts and the accessibility of necessary data.

This paper is focused on fish communities, i.e., groups of interacting swimming macroanimals. Fish communities are an important level to consider in the assessment of fishing impacts for several reasons. First, they are directly impacted by fishing. Large parts of them are direct targets; most other parts are affected through bycatch and discards. Second, whereas much skill has been accumulated for the assessment of populations during one century of fisheries science,

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ecosystem assessment is a new field. Community-scale interactions between populations form the basis of ecosystem structure and function, which are widely recognised as the two components to be concerned about in an ecosystem approach to fisheries management (e.g., Hall 1999; Gislason et al. 2000). Indeed, understanding the natural patterns and dynamics of ecosystems and their robustness to perturbations have long been key questions linking ecological theory to applied ecology (Roughgarden et al. 1989). Hence community assessment is the first step in the building of an ecosystem assessment. Third, more time-series data are available on fish than on other groups, e.g., benthos.

The main effects of fishing on fish populations and communities are broadly known (Jennings and Kaiser 1998; Hall 1999). Fishing will remove older and larger fish from most populations (hence from the community). Even under moderate fishing pressure, this decreases population sizes far below their carrying capacity, and the populations are released from density-dependent regulations. Consequently and to compensate for increased mortality, fish adjust their life history traits such as reproduction and growth. Predators, preys, and competitors are indirectly affected by (and may benefit from) the decrease in number of their preys or predators. As a consequence, the distribution of relative abundance among species often becomes more even, whereas the number of species might be reduced under heavy fishing pressure. Indicators will be variables measuring these effects, which can be estimated.

Most existing community assessment indicators are only sensitive to long-term changes or to the effects of developing fisheries (Jennings and Kaiser 1998; Hall 1999). However, until now scientists have been asked to assess the effects of fishing and of management actions over very short time scales. Typically, single-species assessments are run every year to define annual total allowable catch (TAC). The indicator concept implies a variable that fluctuates and can be used to track progress towards achieving a given management objective; consequently, one specification of indicators is timeliness to allow real-time monitoring of the ecosystem (Garcia and Staples 2000). Hence we are faced with the challenge of assessing fishing effects on ecosystems on the shortest achievable time scale.

For this perspective, we classified indicators into three categories, according to the organisational level considered in the underlying theory. Category 1: indicators for a set of populations, with the population as the basic unit. This is the first step on the way from single-species to community assessment and management: consider together several populations of a community, including nontarget or commercially less important ones. These indicators will be used with the goal of preserving population states, structures, and dynamics. Category 2: indicators for assemblages. The term assemblage is often used to refer to populations living together in a biotope, ignoring interactions (unlike community: Calow 1998). The basic unit is the assemblage: indicators will describe the range of populations and the distribution of their characteristics that may be affected by fishing. While assessing this, the target is to preserve the diversity of the assemblage (in the broad meaning of "variety"). Category 3: indicators for communities, which are considered networks of interacting populations or individuals. These indicators will aim at assessing the effect of fishing on the interactions, the trophic paths, and the biomass flows in the community and will be used for preserving these functions of the community.

We are faced with the challenge of assessing fishing effects on communities that have long been exploited, without knowing their "pristine" state. Hence, we lack data to determine target reference points that could be used as management goals. On the other hand, given the short experience with these indicators, few limit reference points that should trigger management actions are agreed on. In this situation there are three ways of using community indicators. The first one is to give up the idea of using reference points and just examine whether the indicator is currently changing; if fishing is known to cause changes in the observed direction, this can be useful information for management. However, in many cases it will be hard to clearly ascribe the changes to fishing. The second way is to determine theoretical reference points, e.g., by developing a theory for the value of the attribute in an unexploited system and predicting the effect of fishing on it. Here the problem will be to validate a theory to predict system states outside the observed range, be these states desirable or undesirable. Alternatively, an empirical reference system can be developed by gathering indicator estimates from many communities. This needs comparable data on the fish communities and the fishing history. As the community assessment approach is under development, more data will become available, and this approach could be a good future option.

We first present the criteria used for the evaluation of indicators and then review the indicators belonging to the three categories. Based on the outcome of this review, we propose some candidate indicators. To complement this theoretical critique, we tested indicators' performance in a case study (Trenkel and Rochet 2003). Finally, we suggest lines for further research.

Criteria

We evaluated indicators based on four main criteria: meaning, expected effect of fishing, exclusiveness, and measurability.

Meaning

Does the indicator have an understandable relationship with the state and dynamics of animals in the community? This understanding can be based on ecological knowledge or on common sense, which is an asset to indicators to be used by managers and nonscientists in general. However, assigning meaning is subjective and subject to criticism. Hence we were not able to score this criterion in an objective manner, and readers have to make up their own opinion.

Expected effect of fishing

How does the indicator change under the effect of fishing pressure? We distinguished three categories: (*i*) unpredictable indicators; (*ii*) sensitive indicators with a reference direction, some theory allows the prediction of whether the indicator will increase or decrease under exploitation; and (*iii*) sensitive indicators with reference points: the theory underlying or experience with the indicator is so well devel-

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oped that reference values can be defined either as limits that should be avoided or targets that should be aimed at.

Exclusiveness

Is the indicator exclusive to fishing, i.e., is it not expected to vary under the influence of other factors than fishing? We used the underlying theory for identifying exclusive indicators.

Measurability

Is the indicator easily measurable? We examined the data needed for estimating each indicator. We distinguished between those that can be measured from "usually available data" (see below) and those that need additional information.

We used "usually available data" to define a short time series of abundance indices by species and length class (ages are not required), obtained from a scientific survey. Many indicators are based on scientific survey data, because landing data might not be the best information for estimating community indicators. Total catch is often underestimated because of misreporting and discards. Commercial catch is also not representative of the whole community as it is dominated by commercial species, compared with scientific surveys (Rochet et al. 2002). In addition, changes in catches might be driven by changes in fishing practices rather than changes in the exploited community (Caddy and Garibaldi 2000). Furthermore, including sampling variability in indicator estimates is straightforward for survey data (Trenkel and Rochet 2003), whereas uncertainty in catch reports is much more difficult to estimate. We call a "short" time series a series of less than 10 years. Longer time series are difficult to maintain and keep funded. Even if the effort is continued, the series might be inconsistent because of changes (including improvements) in the sampling methods (vessel, gear, sampling design, etc.; see Trenkel and Rochet 2003). Although some problems might arise from the different catchabilities that different species will have in a given survey (Trenkel and Rochet 2003), this cannot reasonably be asked to be known for all examined species.

Indicators

Indicators for populations

The use of fish population characteristics has long been proposed as a holistic approach to ecosystem health assessment (e.g., Shuter 1990). Rather than assessing the population characteristics of one or a few indicator species, monitoring a large sample of representative populations (including noncommercial ones) might be more comprehensive for an ecosystem approach. A tremendous effort has been devoted to the definition and validation of fish stock indicators in use today (see e.g., Smith et al. 1993; Caddy and Mahon 1995). However, these indicators would be difficult to implement for noncommercial species as most of them rely on population dynamics models that require time series of catches and effort, plus additional information such as abundance indices and biological parameters. In contrast, we selected indicators (Table 1) that can be estimated for both commercial and noncommercial species based on minimal information, i.e., the "usually available data" as defined above and in some cases additional data (see below). The associated reference points were also selected to be estimable without too much information, unlike reference points based on stock–recruitment (Bravington et al. 2000) or unfished or virgin biomass (Gilbert et al. 2000). In some cases, noncommercial populations might be positively impacted by fishing, for example, by being relaxed from competition or predation, and this can be inconsistent with setting reference points valid for all. In this section the focus is on harmful effects of fishing at the population level and indirect consequences are neglected.

Population growth rate

Species-by-species tests of change in abundance or biomass have been used for community change assessment using either nonparametric statistics (e.g., McClanahan and Kaunda-Arara 1996) or correlations with time (Haedrich and Barnes 1997) or linear time trends (Heessen and Daan 1996; Jennings et al. 1999). Lotka's intrinsic population growth rate r has also been suggested for fish populations (Quinn and Szarzi 1993). It can be estimated as the slope of log(abundances) against time. If r is significantly lower (respectively higher) than 0, the population is decreasing (increasing). Whichever type of growth rate is used, the expected and undesired effect of fishing is to slow population growth, although many other factors might also have the same effect.

Total mortality rate (Z)

Total mortality rate (Z) is classically written as the sum of natural and fishing mortality rates M and F, and will clearly increase under exploitation. It can be estimated from numbers-at-length data and has been suggested as a robust indicator for exploited populations (Die and Caddy 1997). These authors suggested two reference points for Z, namely Z_{mbp}, which is based on a production model, and Z^*, which takes into account length of catch versus length at maturity, to ensure that total mortality is not so high that fish would die before they reach a sufficient size to reproduce. Estimating Z_{mbp} requires a long times series of population biomass or catch (and accepting the hypotheses of the production model); by contrast, Z^* can be estimated based on biological parameters:

$$Z^* = \frac{(L_\infty - L_m)K}{L_m - L_c}$$

where K and L_∞ are parameters of the von Bertalanffy growth model, L_m is length at first maturity, and L_c is length at first capture. The use of total mortality as an indicator for populations is well founded as it has a clear meaning and predictable effects of fishing, including reference points, but it is clearly not exclusive to fishing impacts.

Exploitation rate (F/Z)

Although it might not be easy to estimate, the proportion of total mortality caused by fishing is an obvious indicator of fishing pressure on a population. We assume here that it can be estimated based on usually available data and a point estimate of total catch (but see Trenkel and Rochet 2003). An F/Z of 0.5 has been proposed as an approximation of F_{MSY}, the target exploitation rate on the basis of production models (Alverson and Pereyra 1969). Clark (1991) found that in most cases F_{mmy}, the target fishing mortality rate based on life history parameters, including consideration of various stock–recruitment relationships, was close to natural

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Table 1. Population indicators for assessing the effect of fishing on a community.

Indicators	Meaning[a]	Expected effect of fishing	Reference point	Exclusiveness	Measurability[b]
Population growth rate r	T	Negative	0	—	+
Total mortality Z	T	Increase	Z^*[c]	—	+
Exploitation rate F/Z[d]	T	Increase	0.5	Yes	Total catch = landings and discards
Average length of population	C	Decrease	—	—	+
Average length of catch	C	Decrease	Length at maturity	—	Total catch = landings and discards
Median age at maturity	C	Decrease	—	—	Age and maturity data
Total lipid energy	T	Unknown	—	—	Condition data
ΔF[d]	T	Decrease	Depends on variability in r	Yes	Age at maturity

[a]Meaning based on common sense (C) or on a theoretical basis (T).
[b]Measurability based on usually available data (+), additional data requirements are listed.
[c]See text for explanation.
[d]F, rate of fishing mortality.

mortality ($F \approx M$). Patterson (1992) used an empirical method and reviewed historical data to recommend that a target $F/Z = 0.4$ would be more conservative for small pelagic stocks, whereas Mertz and Myers (1998) estimated an average F/Z of 0.5 for a selection of pelagic stocks and 0.8 for groundfish stocks. Given these studies, $F/Z = 0.5$ should be considered a limit and stocks considered overexploited when $F/Z > 0.5$. In addition to a clear meaning and the existence of reference points, the exploitation rate can hardly be influenced by factors other than fishing. Its drawback is the need for catch data, which are not always easy to obtain, especially for noncommercial species.

Mean length of catch

A decrease of mean length in the population is expected and has been observed under the effects of fishing (Haedrich and Barnes 1997; Babcock et al. 1999). It can be estimated from usually available data, but it is difficult to define a reference point for it. An alternative indicator is the mean length, or better median length, of catch. The latter needs catch data, but a reference point is available for it. It has been suggested that it should be kept higher than median length at maturity to ensure that at least 50% of all individuals in a cohort spawn at least once (Caddy and Mahon 1995). The question examined is similar to comparing Z with Z^* but can be performed with different data (length structure in the catch instead of total mortality). Other length-based indices frequently used for freshwater fishes include stock density indices, the ratios of the number of fish above specified lengths to the total number of fish in the population (Willis et al. 1993). However, these specified lengths are set from reviews of common lengths of the species in the considered region, which would be difficult to do for marine fishes. Mean length of catch as well as in the population can fluctuate under the influence of environmental factors affecting growth or longevity; hence, they are not exclusive indicators.

Many other possible indicators for populations could be considered in a community perspective: age at maturity (Rochet 2000) or condition indices like the relative weight used in freshwater fisheries (Blackwell et al. 2000) or total lipid energy (Lambert and Dutil 1997; Marshall et al. 1999). All of them may be useful, as long as they can be monitored for a sufficient number of populations. For these indicators, no reference points are currently available. They could be tested for change with the expectation that fishing will decrease age at maturity (Trippel 1995; Rochet et al. 2000). The effect of fishing on total lipid energy is more difficult to predict, as density-dependent effects might counterbalance the decreasing proportion of large fish with high lipid contents.

Indicators for assemblages

There is no doubt that fishing (or any other anthropogenic perturbation) affects community structure and that structure is related to community function. However, the link between the two is far from understood, and structure itself is not clearly defined (e.g., no entry in Calow 1998). Definitions rank from species membership to food web organisation in two chapters of the same handbook (Roughgarden et al. 1989). Often community structure is used interchangeably with species composition, although more recent papers also describe community structure by biological and ecological traits composition. By composition, we mean the nature and quantity of the components (species or species groups or traits) in a community. Here we group indicators that describe the frequencies of elements or the composition of the assemblage without reference to the functions of interest (those to be preserved by management). This has the general consequence that for this group of indicators, desirable or undesirable states that might be used as reference points will be difficult to define. Therefore reference points may only be pristine situations of a comparable assemblage, which is, however, seldom available for exploited marine communities. Hence, for these indicators, looking for fishing effects is mainly looking for changes in indicators: change in time (with continuous or changing fishing) or differences between differently exploited areas (indicators for assemblages are summarised in Table 2).

Species abundance based indicators

Diversity indices

Although there are many ways of describing community

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species compositions, diversity indices have received most attention. Ecologists have long sought a diversity index that would provide a full understanding of community structure in a single number. This has resulted in the development of a large variety of diversity indices (see reviews in Pielou 1975; Washington 1984; Calow 1998), and the developments are still ongoing (e.g., Gray 2000). In as early as 1971, species diversity was termed a "nonconcept" (Hurlbert 1971) on the grounds that the diversity concept is a mixture of species richness and evenness with weightings that are not well justified for most diversity indices, that most existing indices have few if any biological meaning, and that their estimation if often impaired by various technical difficulties (Hurlbert 1971; Washington 1984; Fausch et al. 1990). The latter is especially true for species richness, the estimation of which is sample size and gear dependent (Warwick and Clarke 1996). These arguments are still valid (Washington 1984), even today.

The interest in diversity indices has been renewed by international conventions aimed at preserving biodiversity, together with the ongoing debate on the dependence of ecosystem functions and stability on species diversity (Johnson et al. 1996). Diversity indices are widely used for the assessment of aquatic environments, despite various reports indicating that they are not sensitive to all stress types and that they vary under the influence of natural factors much more than under human impacts (e.g., Washington 1984; Fausch et al. 1990; Allen et al. 1999), including fishing (Rogers et al. 1999). Although many arguments have been put forward that fishing should reduce diversity by selectively removing species (Jennings and Kaiser 1998; Gislason et al. 2000), the usefulness of diversity indices for assessing fishing impacts is questionable (Hall 1999). Decreases in various diversity indices have been found over long time periods (Hall 1999). The opposite has also been reported to be due to evenness increased by fishing down the most abundant stocks (ICES 1996; Rice 2000) or to improved survey and identification methods (Bianchi et al. 2000). If diversity indices are to be used for communicating with customers, as acknowledged by the International Council for the Exploration of the Sea (ICES) Working Group on the Ecosystem effects of fishing (ICES 2000*b*), the Simpson index or the related probability of interspecific encounter (PIE or Δ_1) are appealing because they have direct ecological interpretations (Hurlbert 1971) and do not perform worse than other diversity indices. To sum up, the meaning of many diversity indices is unclear, the effect of fishing on them cannot be predicted, and they are influenced by many other factors. In addition, species richness cannot be measured in most marine communities.

k-dominance curves

The diversity in an assemblage can be described by the distribution of the number of individuals across species, rather than by a single number. Probabilistic models of species-abundance distributions and resource-apportioning models for ranked abundance lists have been developed (e.g., see review in Pielou 1975). However, they are not suitable for exploited fish communities, where resources cannot be assumed to be the limiting factor for population size. Similarly, the assumptions of distribution models are not met as exploitation affects populations selectively. *k*-dominance curves, a plot of the proportion (of total biomass and abundance) of each species against the logarithm of species rank (Clarke 1990), have been tentatively used for fisheries. Their drawbacks are similar to those of diversity indices: most of the time changes are difficult to ascribe to fishing (Rogers et al. 1999). Moreover, interpreting the observed patterns requires a detailed investigation of the information that is aggregated in the index (namely species identification). Although the expected effects of various environmental stresses on the shape of *k*-dominance curves have been described (Warwick and Clarke 1991), the expected effects of fishing remain unclear. Generally speaking, fishing will reduce the size of individuals, hence the biomass-dominance curve should decrease and the abundance-dominance curve should increase, but the magnitude of change will depend on the initial structure of the community and the ranks of the target species. For example, the effect may be opposite if the target of fishing is a small dominant species of the community, as in pelagic fisheries. Before using *k*-dominance curves as ecosystem indicators, the effect of fishing on them should be carefully examined, using an appropriate model. Reference points might be site-specific because of the variety of shapes that *k*-dominance curves have in various environments.

Analyses of species composition

As the interpretation of integrated indices always requires looking in detail at species composition, it would seem more straightforward to directly examine species composition. When large changes occur, the direct examination of species proportions or abundances allows clear conclusions (e.g., Haedrich and Fisher 1996; Quéro and Cendrero 1996). However, in most cases, investigators need multivariate methods such as multidimensional scaling or principal component analysis. The advantage is that virtually the whole information content of the data is kept. Unfortunately, the main result of the analysis is a two-dimensional plot. Most of the time, deciding whether or not two such plots are different is a matter of the author's subjectivity, to say nothing of ascribing the possible changes to fishing or other factors (Jennings and Polunin 1996; Hall 1999; West and Walford 2000). A wider use of resampling methods for comparing ordinations (Manly 1997) is to be commended, as multivariate methods are very popular.

Several methods that might be used to help decide whether patterns found in multivariate analyses differ between areas or periods were recently developed to test for differences in the species composition of a community (e.g., Radach 1998; Collins et al. 2000). They consist of average distance between species compositions, which can be plotted against time or compared for different subsets of the data.

Most of the indicator methods based on species abundance have the drawback of being sensitive to methodological details, such as the distance metric used (Euclidean distance or presence–absence), data normalisation, etc. Some of these indicators may be sensitive, but none is exclusive to fishing effects.

Species trait based indicators

Average traits

There is now a large body of evidence on the effects of fishing on life history traits of populations (see reviews in Jennings and Kaiser 1998; Rochet et al. 2000). By using this approach for the assessment of community impacts, Jennings

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Table 2. Indicators of assemblage properties that might be affected by fishing.

Indicators	Meaning[a]	Expected effect of fishing	Measurability[b]
Species richness	C	—	—
Species diversity e.g., Δ_1	T	—	+
k-dominance curves	T	To be determined	+
Ordination of species abundances	T	—	+
Species composition	C	—	+
Average growth rate	T	Increase	Age data for many species in the community
Average maximum length	C	Decrease	+
Average age at maturity	T	Decrease	Age and maturity data for many species in the community
Average size at maturity	T	Decrease	Maturity data for many species in the community
Mean length distribution	C	Pristine: log uniform or right-skewed Exploited: shifted to the left	+
Size–abundance relationship	T	Pristine: linear with negative slope Exploited: decreased slope	+
Ordination of species traits	T	Smaller and faster traits	Species trait data

[a]Meaning based on common sense (C) or on a theoretical basis (T).
[b]Measurability based on usually available data (+), additional data requirements are listed.

et al. (1999) found that in the North Sea fish community average growth rate increased, whereas average maximum size, age at maturity, and size at maturity decreased (see also ICES 2001*a*). This conforms to the expectation that fishing should (*i*) change these parameters within populations and (*ii*) favour populations with particular traits.

Trait distribution

Looking at distributions across populations rather than simple means should improve our insight. The combination of the individual population responses to fishing will show up as distribution of traits in a way that is not yet known but would improve our understanding of the adaptability of communities. The shape of the distribution of species numbers per size class has attracted much attention (Blackburn and Gaston 1994). For some vertebrates, these distributions have been found right-skewed at continental scales and more uniform at local scales (Brown and Nicoletto 1991). Other authors have examined the relationship between population density and body size (Schmid et al. 2000). The three dimensions may be linked and should be looked at together (Lawton 1989). The underlying idea is that there are laws governing the assembly of communities, but the supporting theory is very general and based on resource-partitioning ideas (Brown et al. 1993). To apply this kind of model to exploited fish communities would require a theoretical approach on the way that fish partition resources and the effect of fishing on this partitioning. A possible effect of fishing on the intercept of the relationship between species richness and population density was found in the North Sea (Hall 1999). Currently this approach can be used in a comparative manner only: did the distribution of sizes or the size–abundance relationship change? The expected effect of fishing is a shift towards smaller species and a steeper slope of the size–abundance relationship. As species richness is highly influenced by sampling methods and responds in the longer term, adding this third dimension requires a long time series of data collected with a consistent sampling method. The expected effect of fishing is to reduce species richness at any size and density.

Trait ordination

For biomonitoring stream communities, another approach using species traits was developed (Charvet et al. 2000; Usseglio-Polatera et al. 2000). Species biological and ecological traits like body size, life span, body form, diet, reproduction, distribution, or substrate are categorised and analysed together in a multivariate analysis weighted by species abundance. This method was found to be a better tool for describing the impact of pollution on a stream community than the analysis of species composition or diversity indices. It has been also used for marine benthic communities (Frid and Robinson 2000). So far this is a purely empirical approach and the question examined is, did the trait composition of the community change? Fishing is expected to shift the community towards smaller and faster traits and the geographic distribution to areas less accessible to fishermen. In freshwater environments it has been suggested to develop a "reference-condition" approach by typifying diversely impacted rivers by some combination of biotic traits (Charvet et al. 2000). However, such developments for the marine environment would probably require much more data than available.

Trait-based indicators are on the way to being developed. Despite the lack of experience in this field, they might be a promising track because the effects of fishing on many traits can be predicted, although environmental forcing might obscure them: none can be said to be exclusive to fishing effects. Another drawback is their high data demand. Further research should focus on the most easily measured traits such as length.

Indicators for communities

This section deals with indicators measuring the functions expected from the community themselves rather than some

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presumably related patterns (Table 3). These functions are producing biomass, transferring biomass from low to higher levels, and producing large valuable fish. However, communities are more abstract concepts than populations and have generated diverse theories describing their processes and functioning. Identifying theories useful for fisheries effects assessment is the purpose of this section.

Total biomass

If biomass production is expected from a community, a simple and obvious indicator of this function is total fish biomass or abundance. A biomass decrease in the community would impair the productivity of dependent fisheries. On the other hand, the effects of fishing on total fish biomass are difficult to predict because of indirect effects along food webs. For example, the total fish biomass in the Baltic Sea increased during the 20th century, presumably because of eutrophication and relaxation of predation by exploited top predators (Thurow 1997). The same applies to total abundance.

It has been suggested that increased temporal variability in various indicators might be a sign of stress in communities (Warwick and Clarke 1993). For example, biomass variability has been proposed as an indicator of fishing pressure (Duplisea et al. 1997) based on the assumption that exploitation should release interspecific competition, which is supposed to stabilise total biomass (Holmgren 1999). However, this is rather theoretical and there is weak field evidence to support this assumption. Moreover, estimating variability requires much longer time series data than estimating means, and disentangling true variability from time trends is not easy and has already proven confusing (Pimm and Hyman 1987). Therefore, indices of temporal variability are not promising indicators, but this does not mean that the variability in any indicator should not be taken into account when assessing this indicator's value.

Trophic composition

Not all biomass is equivalent and the definition of the function expected from the community might be refined to producing large fish or to producing large predatory fish. However, the use of one or few "indicator species" such as top predators is not advisable for several reasons. The causes of their absence are variable and not well defined, their sensitivity to human impacts will vary between regions or environments, and the response is binary: a species is present or absent (Fausch et al. 1990). Alternatives used as components of stream fish community assessment are attributes describing their trophic composition (Fausch et al. 1990; Miller et al. 1998), such as the proportion of omnivorous individuals in the community, of top carnivores, or of generalised feeders, depending on the local context. Similarly, changes in the trophic composition of marine communities can be tested in terms of large trophic groups such as planktivorous, benthivorous, or piscivorous animals (Caddy and Garibaldi 2000). The expected effect of fishing (although not exclusive) is a decrease in the proportion of piscivorous fish. This is an easily understood indicator that can be estimated based on the knowledge of the biology of the species present in the community rather than on extensive diet data. A related index that has been proposed as an indicator for marine environments is the pelagic (P) to demersal (D) fish biomass ratio in fishery landings (Caddy 2000; de Leiva Moreno et al. 2000). However, the P:D ratio in fisheries catches is not exclusive in that it might be an indicator of eutrophication rather than exploitation (de Leiva Moreno et al. 2000). In addition, like other catch-based indicators, it will be sensitive to changes in the fishing targets and methods.

Food web models

There are many models, methods, and theories for food webs or chains (e.g., see review in Roughgarden et al. 1989) from which indicators could be derived. The first step in analysing a food web is to examine its trophic structure, i.e., the trophic links between species. To make the model tractable, species are often clustered into trophospecies, which are groups of species with common food and predators. This clustering has a strong influence on the results of subsequent analyses (see below). Methods are being developed to perform the clustering but they cannot yet be standardised (Yodzis and Winemiller 1999). Static analyses looking at connection and the diversity of paths or fluxes may lead to indicators of ecosystem maturity or functioning (e.g., Puccia and Levins 1985; Pérez-España and Arreguín-Sánchez 1999). However, they are strongly biased because many species and trophic links are poorly detectable in the field (Goldwasser and Roughgarden 1997), and they are highly sensitive to species aggregation in trophospecies (Paine 1988). Dynamic models of food webs have been criticised because they do not describe many important and complex features of real food webs such as omnivory, life history, nutrients, pathogens, etc. (Polis and Strong 1996). Even if more realistically complex, dynamic models might not be very useful because effects of changes in food webs are indeterminate: it is not possible to predict which species will be favoured or impaired by a perturbation (Yodzis 1988). Effects of changes are also diffuse, which means that they attenuate through trophic interactions involving many species (Yodzis 2000). These theoretical results are confirmed by the available evidence from marine pelagic ecosystems (Micheli 1999).

The problems encountered in food web modeling make the approach unsuitable for measuring fishing impacts in the marine environment. Because of the tradeoff between complexity imposed by realism and simplicity necessary for precision, numerical predictions using models of predation in marine fisheries are unreliable in most cases (Bax 1998). Marine food webs have several characteristics that highly influence their dynamic properties: life history omnivory (the change of prey when individuals grow, Pimm and Rice 1987), intraguild predation, wasp-waist control (as opposed to top-down or bottom-up, Rice 1995), and variability on many time scales (Rice 2001). Taking all these aspects into account would make models intractable, and the idea that the long-term behaviour of marine ecosystems is unpredictable is pervading. As an example, despite the huge efforts put into the development of the multispecies virtual population analysis (MSVPA) model for the North Sea, MSVPA is not used directly for fisheries management but rather for estimating natural mortality rates that are then included in single-species assessments of North Sea fish (Magnússon 1995). MSVPA makes very strong assumptions about ration size and food preference, which are matter for debate (Bax

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Table 3. Indicators of community properties that might be affected by fishing.

Indicators	Meaning[a]	Expected effect of fishing	Potential reference point[b]	Exclusiveness	Measurability[c]
Total biomass/ abundance	C	—	—	—	+
Biomass variability	T	Increase	—	—	Long survey data series
Proportion of piscivorous fish	C	Decrease	C	—	Approximate species diet
Pelagic to demersal ratio (P:D)	T	Increase	—	—	Species habitat
Trophic structure descriptors	T	—	—	—	Accurate diet of all species and their prey
Mean trophic level	T	Decrease	C	—	Accurate diet or $\delta^{15}N$ of all species and their prey or biomass of all ecosystem components
Fishing in balance (FIB)	T	Decrease	T	Yes	Idem and catch time series
Proportion of noncommercial species in the community	C	Increase	T, C	Yes	Knowledge of commercial species
Average weight in the community	C	Decrease	—	—	+
Size spectrum	T	Fewer large fish/less total biomass	T, C	—	+

[a]Meaning based on common sense (C) or on a theoretical basis (T).
[b]Reference point potentially defined based on theory (T) or on comparative data (C).
[c]Measurability based on usually available data (+), additional data requirements are listed.

1998), and only includes the parts of the food web that are well known, the remainder being fixed. These assumptions are so restrictive that MSVPA could not be extrapolated to any other system (Magnússon 1995). Another example is the large effort devoted to assess the competition between fisheries and top predators, of which the main conclusion is that we still do not know whether culling top predators would be beneficial to fisheries (Yodzis 2001). To summarise, whatever model is used to describe the trophic structure of a community, the effects of fishing remain unpredictable, and there is not much to be expected from future developments.

Trophic level

A proposed indicator of the effect of fishing on food webs is the mean trophic level of fisheries catches, which decreased at the global level during the last decades (Pauly et al. 1998). Unfortunately, mean trophic level of catches is not a good indicator of the effects of fishing on communities, because it may be biased by economic incentives and technological advances (Caddy et al. 1998; Caddy and Garibaldi 2000). Instead, the mean trophic level in the community might be used. Although the trophic level concept was criticised as fictitious because of food web complexity (Polis and Strong 1996), it still has some intuitive appeal. Currently, trophic level can be estimated by three methods. Gut content analyses are known to be biased by regurgitation and differential digestion times (Bowman 1986; Pinnegar et al. 2002). This method also needs a large amount of data collection and analysis because of highly variable diets and includes the investigation of trophic levels of every prey item. Trophic levels can also be obtained as output of mass balance models (such as ECOPATH, Polovina 1984), but these models rely on mostly unverified equilibrium assumptions and require quite extensive data for which consistent quality and reliability is difficult to achieve. In addition, mass balance models are also sensitive to the taxonomic aggregation of the trophic web model (Caddy et al. 1998; Pinnegar et al. 2002). The third method, the analysis of stable isotopes of nitrogen, relies on the assumption that $\delta^{15}N$ in organisms is enriched at each trophic level by 3.4‰ (Vander Zanden et al. 1997; Post et al. 2000; Pinnegar et al. 2002). However, this increment is an average and ^{15}N enrichment is highly variable among tissues, individuals, species, and trophic levels (Minigawa and Wada 1984; Owens 1987). The level of $\delta^{15}N$ is also known to vary between samples and over time within individuals, among individuals, and among ecosystems for diverse reasons (Owens 1987; Vander Zanden et al. 1997; Post et al. 2000). Before claiming that mean trophic level in the community might be a sensitive indicator of fishing effects (Pinnegar et al. 2002), the magnitude, causes, and consequences of this variability should be carefully examined and an appropriate methodology should be developed (for an appropriate model of ^{15}N enrichment see Owens 1987). Therefore, reliable methods for measuring trophic levels are currently not available. Nevertheless, this indicator is attractive because the reference direction is obvious. Given the large data demands, its use will probably be restricted to special cases.

Fishing in balance (FIB), a related indicator designed to "assess whether a fishery is balanced in ecological terms", requires in addition to accept the hypothesis that transfer efficiency is constant across trophic levels and known (Pauly et al. 2000). Comments similar to those just made on mean trophic level equally apply to this indicator.

Size spectrum

There is strong evidence that predation in the marine environment is not species dependent, but rather size dependent. A fish can eat any fish, provided it is in the appropriate size range. Indicators based on this kind of assumption are re-

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lated to size spectra. It was noticed a long time ago that aggregated length distributions of all fish individuals obtained from scientific surveys are regular and conservative and may therefore be used as indicators for exploited communities in various environments (Pope and Knights 1982; Murawski and Idoine 1992). These authors recognised that size spectra characteristics may vary between ecosystems and that fishing should affect them by removing large fish and possibly thereby enhancing small fish relaxed from predation. Considering that in a middle size range, the size spectra seem linear, it has been inferred that fishing may make their slope more steeply negative and possibly increase their intercept. Indeed such time trends have been found in the North Sea and Scotian Shelf (Rice and Gislason 1996; Bianchi et al. 2000). However, in six other systems with sufficiently long time series examined by Bianchi et al., no such trends were found. In the Benguela system, slopes of size spectra differed between areas of different productivity but were not affected by fishing (Macpherson and Gordoa 1996). The linearity of size spectra, even in a reduced size range, might be questioned when looking at most data series. In addition, ordinary fitting methods yield correlated estimates of slopes and intercepts (as reported by, e.g., Bianchi et al. 2000), and this effect might be enhanced if the linear model is inappropriate. Indeed, some authors examined dome-shaped models of fish size spectra (Duplisea et al. 1997). In summary, because of methodological difficulties and despite accumulated experience, it is currently not possible to state precisely how fishing affects size spectra. Simulations have shown that fishing should affect slopes and intercepts of size spectra considered linear, using a MSVPA model (Rice and Gislason 1996; Gislason and Rice 1998) or an individual-based model where predation processes depend on size (Shin 2000). Simulations with the latter model also showed that fishing might increase the curvature of size spectra described by a quadratic model. However, the relationship between the magnitude of simulated effects and the parameters used for simulations was not investigated. Further theoretical work and examination of data from various areas with appropriate methods are still needed. Every study analysing size spectra will be useful in accumulating experience provided that (*i*) the size range used for model fitting is not arbitrarily set but determined by the size range with consistent catchability by the sampling gear and (*ii*) slope and intercept estimates are not spuriously correlated, which can be avoided by centering the independent variable.

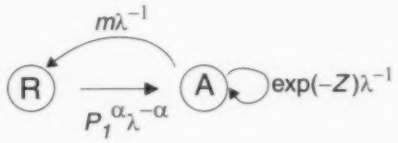
Some proposals

Based on the previous considerations, we propose one more population indicator and two simple indicators for communities. Like all existing community indicators, the latter do not have associated reference points; however, the reference directions are clear.

ΔF: change in fishing mortality required to reverse population growth rate

This is an indicator for population sensitivity to fishing. The population growth rate r indicates whether a population is declining and F/Z indicates how much fishing mortality contributes to total mortality. However, depending on their life history, species might be able to sustain different fishing mortalities. We propose an indicator for this based on the elasticity of population growth rate to fishing mortality. Elasticity measures the proportional change in $\lambda = \exp(r)$ that would result from a change in F, all other parameters being fixed. Consider the simple population model with two stages: recruits and adults (Fig. 1).

Fig. 1. Life cycle graph for a two-stage population model: R, recruits; A, adults; P_1, annual survival of recruits; Z, adult mortality rate; m, annual fecundity; α, age at maturity; λ, population growth rate.



Following Caswell (2001), the characteristic equation of this life cycle is

$$\lambda^{\alpha+1} - \exp(-Z)\lambda^{\alpha} - P_1^{\alpha} m = 0$$

The real root λ of this equation is the population growth rate. The contribution of fishing mortality F to λ (also known as the elasticity of λ to F):

$$e_F = \frac{F}{\lambda}\frac{\partial\lambda}{\partial F} = \frac{F}{\lambda}\frac{\lambda\exp(-Z)}{\alpha\exp(-Z) - \lambda(1+\alpha)}$$

can be estimated knowing only Z, F, α, and λ (Heppel et al. 2000). Hence this indicator answers the question, would the population dynamics be sensitive to an increase in fishing mortality? This can be examined, taking account of the precision of the available information, by the following steps: (*i*) compute elasticity e_F; (*ii*) use e_F, which can be interpreted as the slope of $\log\lambda = r$ against $\log F$ (Caswell 2001), to estimate ΔF, the change in F necessary to make the population significantly decrease (for stationary or increasing populations) or necessary to stop the decrease (for decreasing populations); and (*iii*) compare this change with a predefined limit. To establish this limit, the variability of VPA-estimated F (averaged over relevant age classes) was examined during periods without apparent trend in fishing mortality for various stocks in the Celtic and North seas (Table 4). Based on this review, the fishing mortality applied to many stocks fluctuates from year to year with a coefficient of variation of 15–20%. Hence it would not be reasonable to consider significant a variation lower than 20%. Therefore the limit for ΔF is set at 20%. If ΔF is lower than 20%, then the population will be said to be sensitive to fishing mortality. Alternatively, at least for exploited and regularly assessed populations, the limit might be defined based on the historic variability of F in the considered population.

This indicator is data demanding and is not an indicator of fishing impact, but of the potential effectiveness of management actions. As such, its meaning is complementary to other population indicators. It is rather exclusive to fishing effects, and a reference point is relatively easily set. The more populations are sensitive to fishing in a community, the more it is worth reducing fishing mortality.

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Proportion of noncommercial species

On the grounds that in exploited communities, commercial species decrease in abundance (Haedrich and Fisher 1996; Babcock et al. 1999), whereas noncommercial species remain unchanged (Greenstreet and Hall 1996) or even increase (Heessen and Daan 1996; Hall 1999), we propose that the proportion of noncommercial species in the community should increase as a result of exploitation. Hence a simple test for change in species composition attributable to fishing is to compare the proportion of noncommercial species over time. If the period is long, the commercial status of some species might change (Sumaila 1998); hence, the test should keep as noncommercial all species initially in this status. A test for a time trend in this proportion can be carried out. This is an easily understood and measurable indicator that is rather exclusive to fishing, but finding theoretical foundations for setting reference points would be difficult, and those would have to be defined empirically based on historical data.

Mean length and weight in the community

A simple indicator related to size spectra that might be easy to estimate and interpret is the mean size (measured by length or weight) of individuals in the community, which is expected to decrease in exploited populations as do mean lengths of individual populations. However, its sensitivity to environmental forcing is not yet well known, which makes the prospect of finding reference points uncertain.

Conclusions

The art of assessing the impact of fishing on biological communities is still in its infancy. Although a large variety of indicators have been developed, few have been validated, very few have associated reference points, and still fewer could be delivered to managers for use in decision making. The most operational ones are those for populations. It has been argued that currently integrative community and ecosystem indicators are not developed enough to be used as tools for achieving ecosystem objectives. Instead, monitoring and defining goals for a wide selection of species might be the only possible approach for some years to come (ICES 2000*b*). Although this seems the best possible way at present, the drawback is that keeping all populations within reasonable boundaries is not a guarantee to preserving ecosystem structure and function, although it seems a step in the right direction. Hence further developments aimed at a more comprehensive picture of communities are needed. Indicators for assemblages appear to be the least convincing ones because their interpretation is rarely straightforward and because potential theoretical foundations to develop reference points or merely predict directions of change are weak. Nevertheless, these indicators are descriptive tools that may be used to compare areas rather than for a proper assessment. Enriching species diversity with trait diversity would probably improve the description. It would also be a step towards more functional indicators. Indicators for communities appear to be a more promising track, although much work is still to be done. We need theories for size spectra and for robust and synthetic characteristics of food webs that are not too sensitive to the details of the measurement methods and analyses. For all of them, much theoretical and analytical work is required to design reference points; in this respect, much will be gained from accumulating empirical experience. There are probably many other ways of assessing the impact of fishing on community functions that we overlooked or that are still waiting to be invented.

Because exploited communities are complex systems and because very few indicators are exclusive to fishing impacts, finding a single indicator that measures the effect of fishing will be difficult. An alternative approach is to examine multiple indicators to accumulate evidence (Garcia and Staples 2000; Rice 2000). However, this immediately raises the question of how to summarise the information provided by a set of indicators. To our knowledge, few methods are available. Garcia and Staples (2000) suggest graphical methods like kite diagrams. Stochastic–dynamic kites allow the depiction of uncertainty and trends in indicators. Multivariate analyses have also been proposed (Pitcher et al. 1998; Link et al. 2001). A third method is the aggregation of indicators into composite indices, like the indices of biological integrity (IBIs) used for freshwater monitoring. The latter are designed to translate a full ecological assessment for persons unfamiliar with ecology (Hughes et al. 1998). Within IBIs, indicators are scored into levels of community disturbance using criteria that depend on assemblage structure and function of regional stream fish faunas and their response to environmental stress (Miller et al. 1998). In any case, fundamental difficulties lie in the necessary weighting of indicators. For example, if all populations keep within safe limits but mean length in the community is steeply decreasing, which information should be considered the most important? Giving all indicators the same weight is far from neutral: the outcome will depend on the number of indicators aggregated and on their relative sensitivity, even if they are standardised to some common measure. Also the standardisation method will influence the final result. Any aggregation will be related to the "value" attached to each component examined. The problem is complicated by the redundancy and overlap of indicators and their different units. However, weighting systems go beyond the scope of this paper; this is another field where developments are strongly and urgently needed.

We have selected and appraised indicators using several criteria. Some indicators were also tested by an application to the Celtic Sea (Trenkel and Rochet 2003); however, each indicator needs further validation. Most studies in this field have used comparative approaches by gathering estimates of indicators from various systems and trying to find general patterns (e.g., Bianchi et al. 2000) or by correlating various indicators supposed to give similar information (e.g., Pérez-España and Arreguín-Sánchez 1999; de Leiva Moreno et al. 2000). This approach is most powerful when neighbouring areas with contrasting exploitation rates (Jennings and Polunin 1996) or a given system before and after exploitation (Frid and Robinson 2000) can be compared. However, this is seldom possible in marine systems that are heterogeneous and in which sampling generally began long after fishing. In this respect, the development of marine protected areas will give opportunities to validate community indicators (e.g., Babcock et al. 1999). Statistical methods have been used to make comparative approaches more powerful, namely meta-analysis (Myers and Mertz 1998; Englund et al. 1999). If

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Table 4. Coefficient of variation (CV) of fishing mortality rates *F* averaged over relevant age classes (adults/exploited phase) during periods with no trend in *F*.

Stock	Period	CV (%)
Celtic Sea anglerfish (*Lophius budegassa*)	1992–1997	20
Celtic Sea anglerfish (*Lophius piscatorius*)	1992–1998	18
Celtic Sea megrim	1992–1998	8
Celtic Sea *Nephrops norvegicus*	1989–1997	6
Celtic Sea plaice	1984–1998	17
Celtic Sea sole	1994–1999	9
Northeast Atlantic hake (W. stock)	1992–1998	21
Northeast Atlantic horse-mackerel (W. stock)	1992–1997	33
Northeast Atlantic mackerel (W. stock)	1975–1991	16
North Sea cod	1980–1994	7
North Sea haddock	1970–1993	12
North Sea Norway pout	1977–1987	17
North Sea whiting	1965–1991	19

Note: Sources of *F* estimates: reports of ICES Stock Assessment Working Groups (ICES 1999, 2000*c*, 2000*d*, 2001*b*). W., western.

sufficient situations are to be compared, the variance and distribution of indicators can be measured for a better appraisal of their sensitivity (Holmgren 1999; Micheli 1999). Meta-analysis can also be used to estimate reference points for a given indicator (Patterson 1992) or to develop scoring systems for IBIs (Hughes et al. 1998; Miller et al. 1998). If many indicators or multidimensional indicators are considered together (e.g., population indicators), multivariate techniques can be used to define reference systems (Pitcher et al. 1998; Charvet et al. 2000; Link et al. 2001). This requires the availability of data from "reference situations" (at least overexploited or less exploited situations). In addition, there is still work to be done to make this highly integrated information understandable to the managers and the public. An alternative method for validating indicators and setting reference points would be the development of community or ecosystem models to generate data with known fishing pressure (Pitcher et al. 1998). This has been extensively used for single-stock indicators. However, ecosystem models are much more complex and suffer from many of the problems listed above. For obvious reasons, models built to validate an indicator should, however, not rely on the same assumptions as the indicator itself. This will not be an easy job.

There is still much to be done in developing indicators of fishing impacts on fish communities. Although all tracks are not similarly promising, many of them should be explored and indicators improved. There is an urgent need to incorporate science in the assessment process to avoid the prevalence of irrational and prejudiced views.

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PERSPECTIVE

Assessment of net change of productive capacity of fish habitats: the role of uncertainty and complexity in decision making

Charles K. Minns and James E. Moore

Abstract: Canada's fish habitat management is guided by the principle of "no net loss of the productive capacity of fish habitat" (NNL). Many development proposals are assessed using habitat information alone, rather than fish data. Because fish–habitat linkages are often obscured by uncertainty, uncertainty must be factored into NNL assessments. Using a quantitative framework for assessing NNL and lake habitats as a context, the implications of uncertainty for decision making are examined. The overall behaviour of a net change equation given uncertainty is explored using Monte Carlo simulation. Case studies from Great Lakes development projects are examined using interval analysis. The results indicate that uncertainty, even when large, can be incorporated into assessments. This has important implications for the habitat management based on NNL. First, schemas to specify relative levels of uncertainty using simple habitat classifications can support robust decision making. Second, attaining NNL requires greater emphasis on minimizing habitat loss and creating new areas to compensate for losses elsewhere and less on detailing small incremental changes in modified habitats where the fish response is difficult to demonstrate. Third, the moderate to high levels of uncertainty in fish–habitat linkages require that created compensation is at least twice the losses to reasonably ensure NNL.

Résumé : La gestion des habitats de poissons au Canada suit le principe selon lequel il ne doit y avoir « aucune perte nette (NNL) de capacité de production des habitats de poissons ». Plusieurs projets de développement sont évalués d'après les seules données de l'habitat, plutôt que d'après des données sur les poissons. Puisque les liens entre les poissons et les habitats sont souvent obscurs à cause de l'incertitude, cette incertitude doit être prise en compte dans les évaluations NNL. L'utilisation d'un cadre quantitatif pour évaluer NNL dans le contexte d'habitats lacustres nous a permis d'examiner les implications de cette incertitude dans le processus de décision. Le comportement d'une équation de changement net en présence d'incertitude a été étudié à l'aide d'une simulation de Monte Carlo. Des études de cas de projets de développement dans le Grands-Lacs ont été examinées à l'aide de l'analyse d'intervalles. Nos résultats indiquent que l'incertitude, même importante, peut être incorporée aux évaluations. Cela a d'importantes implications pour la gestion des habitats basée sur NNL. Premièrement, des schémas servant à spécifier le niveau d'incertitude à partir de classifications simples de l'habitat peuvent permettre des prises de décision sûres. Deuxièmement, lorsque la réaction des poissons est difficile à démontrer, l'atteinte de NNL nécessite une emphase plus grande sur la minimisation des pertes d'habitat et sur la création de nouveaux habitats pour compenser les pertes subies ailleurs, que sur de petites améliorations successives dans les habitats modifiés. Troisièmement, à cause des niveaux d'incertitude moyens à élevés qui existent dans les liens entre les poissons et les habitats, il faut que les habitats créés en compensation correspondent à au moins le double des pertes pour pouvoir raisonnablement assurer NNL.

[Traduit par la Rédaction]

Introduction

It is vital that conservation and protection practices for fish habitat resources be based on scientific principles and knowledge. Canada's policy for the management of fish habitat (DFO 1986) is embodied in its guiding principle of "no net loss of the productive capacity of fish habitat" (NNL). Productive capacity is defined as "the maximum natural capability of habitats to produce healthy fish, safe for human consumption, or to support or produce aquatic organisms

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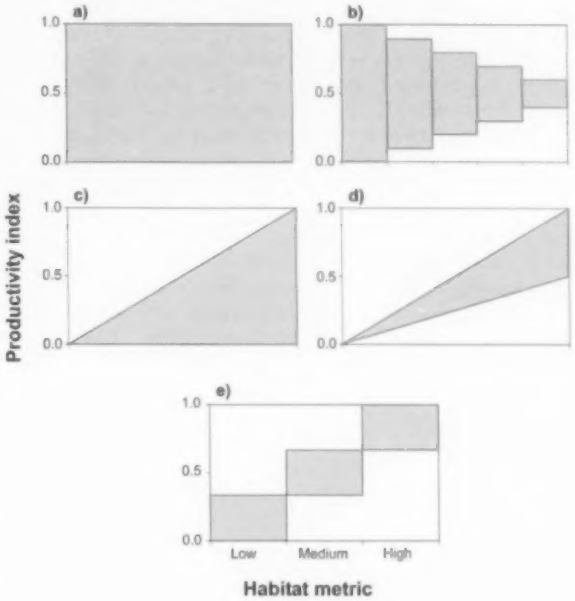
upon which fish depend" (DFO 1986). Minns (1997) proposed a quantitative basis for assessing net change of productive capacity, based in part on the habitat evaluation procedures (HEP) used in the United States (Terrell et al. 1982). Assessments of net change have been conducted assuming that the areas and productive capacity indices used to characterize fish habitats have fixed and known values. Where uncertainty as the result of temporal or spatial variation and imperfect information is considered, it is usually done by informal and nonquantitative methods. Hence, the significance of estimated gains or losses is unclear to fish habitat managers. Uncertainty needs to be considered in assessments used for decision making (Morgan and Henrion 1990) and specifically for development proposals affecting habitat (Burgman et al. 2001). Fixed-value estimates can be misleading. The goals of this paper are (*i*) to examine the role of uncertainty, and the associated issue of the complexity of habitat classifications (i.e., how many different levels or ranges of habitat productivity are defined), in determining net change outcomes, (*ii*) to recommend for fish habitat managers an initial operational approach to decision analysis with uncertainty for fish habitat management in Canada, and (*iii*) to draw some inferences for policy makers on ways to attain NNL.

At present, most fish habitat management decisions under the Fisheries Act in Canada involve considerable uncertainty. The uncertainty is mainly centred on fish–habitat relationships and has three sources: (1) the incomplete state of knowledge about such relationships; (2) high levels of natural variation in biological and environmental conditions that obscure relationships; and (3) human mistakes in inferring and (or) assessing relationships. Much of the uncertainty arises from ignorance rather than from natural variation, although the latter makes a substantial contribution. This is because most assessments have access to very little site-specific or development activity specific information, and our knowledge is rudimentary in most instances, apart from a few well-studied species (Auster 2001; Minns 2001). Often cross correlations among many habitat and fish metrics further complicate the situation.

Rose (2000) reviewed efforts to elucidate relationships between habitat and fish populations and pointed out the difficulties experienced and a range of reasons why clear relationships are elusive. The relationships between habitat and fish metrics can take many forms (Fig. 1). The uncertainty in basic fish–habitat relationships was highlighted by Terrell et al. (1996), who drew attention to the prevalent "wedge-shaped" patterns seen in stream fish studies. (Wedge-shaped patterns are usually seen as a wide scattering of points in the right triangle below a line between the origin and the maxima in habitat (*X*) versus fish (*Y*) metric plots as in Fig. 1*c*.) Measurement and ecological factors on both axes contribute to these patterns. The diversity of patterns that can arise from mixing fish sampling techniques can further cloud relationships (Jackson and Harvey 1997). Wedge-shaped patterns have been reported in lakes (Randall et al. 1996). This is part of a widespread phenomenon of scattergram relationships seen often in ecological studies (Scharf et al. 1998). These wedge-shaped patterns contribute strongly to the limits set on the number of discrete classes that can be discriminated in a relationship. Prairie (1996) showed how discrimination of more than 2–4 classes requires exceptionally high coefficients of determination (>0.7–0.8), levels rarely encountered in field studies of fish–habitat associations. The confounding of habitat variables undoubtedly adds to these difficulties.

Fig. 1. Diagrams showing the five productivity uncertainty patterns used in the Monte Carlo simulations of net change of productive capacity: (*a*) completely random, (*b*) bounded random, (*c*) wedge random, (*d*) spread random, and (*e*) no overlaps, three bands. The shaded areas represent the zones in which sample values might be expected to occur.



The complexity considered here primarily relates to the habitat classifications used to represent the range of fish habitats present in ecosystems. Classification is important because it reflects in fish habitat management decision making how uncertain fish–habitat relationships are represented. Available evidence points to greater classification success when fewer habitat types are delineated (Frezza and Minns 2002). Habitat classifications can vary considerably in their complexity. In both streams and lakes, habitat features include depth, substrate, and cover, each of which has a continuum of values. In streams, water movement is usually indicated by current velocity, whereas in lakes, water movement is usually inferred from fetch or exposure indices. Studies at the present time often exploit the overlay capability of geographic information systems, generating complex classifications. Arbitrary division of several continuous habitat variables into ranges can generate extensive classification schemes in lakes, but often habitat variables are convoluted and the set of combinations that actually occurs is often limited. It is not possible to discriminate among many habitat classes with available fish knowledge and data. Conversely, in assessing lake development projects, biologists from Fisheries and Oceans Canada (DFO) often rely on limited numbers of classes, as proponent investments in habitat surveys are minimal, typically less than 10 and often less than five classes (C.K. Minns, personal observation). Field investiga-

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tions of fish–habitat associations within lakes are often presented with limited sets of habitat types, based on analyses that indicate few discriminable sets of sites or samples (e.g., Keast et al. (1978) in Lake Opinicon; Fischer and Eckmann (1997) in Lake Constance). In streams, the simple pool–riffle–run system, and its variants, has provided considerable utility in discerning fish–habitat relationships (e.g., Aadland 1993; Jowett and Richardson 1996). Willis and Magnuson (2000) described a simple grouping of habitat types in relation to fish associations in stream–lake systems. These field observations point to limited sets of habitat types. If fish habitat management decisions are going to rely on classifications with few classes, assessments of uncertainty must be developed in that context. Also, because mandating the use of complex habitat classifications adds considerably to the baseline assessment costs for development proponents, it is important to determine how much impact classification complexity per se might have on net change based decision making.

Thus, the available evidence, empirical and statistical, indicates that simple habitat classification systems with few classes may provide a workable basis for assessment of net change of productive capacity even though the uncertainty within classes and the overlap between classes may still be relatively high. The simulation analyses and synthesis presented here explore the consequences of high uncertainty in fish–habitat linkages and low classification complexity with regard to the potential effectiveness of decision making under Canada's fish habitat policy.

Materials and methods

Two uncertainty modelling approaches are used: (*i*) Monte Carlo simulation to assess how net change is affected by uncertainty and (*ii*) interval analysis (Moore 1979) to examine how uncertainty affects case studies (individual examples where net change is assessed for decision making). We have taken assessment of NNL in lake habitats as a context for this presentation, but the results should be applicable in the oceans and somewhat in streams and rivers when flow alteration is a minor issue. Application of the defensible methods approach (Minns and Nairn 1999; Minns et al. 2001) provides case studies for some of the analyses used as illustrations.

Model of net change of productivity of fish habitats

Minns (1997) described an equation for assessing net gain or loss of natural productivity of fish habitats, i.e., productive capacity. Net change is computed as follows (based on eq. 15 in Minns 1997):

$$(1)\quad \Delta P_{NOW} = (p_{MODD} - p_{NOW})A_{MODD} + (p_{MODI} - p_{NOW})A_{MODI} - p_{MAX}A_{LOSS} + (p_{COMM} - p_{NOW})A_{COMM} + p_{COMC}A_{COMC}$$

where ΔP_{NOW} is the net change of natural productivity of fish habitat, A_{LOSS} is the area of habitat loss resulting from development activity, A_{MODD} is the area modified directly as a result of the development activity, A_{MODI} is the area modified indirectly as a result of the development activity, A_{COMM} is the area modified elsewhere to compensate for the development activity, A_{COMC} is the area created elsewhere to compensate for the development activity, p_{MAX} is the maximum potential unit-area productivity rate or productive capacity, p_{NOW} is the present unit-area productivity rate, p_{MODD} is the modified unit-area productivity rate in directly affected areas, p_{MODI} is the modified unit-area productivity rate in indirectly affected areas, p_{COMM} is the unit-area productivity rate in existing habitat areas modified as compensation for losses elsewhere, and p_{COMC} is the unit-area productivity rate in habitat areas newly created as compensation for losses elsewhere.

The unit-area productivity rates, p, are expressed as proportional values between zero and one and are typically derived as habitat suitability indices (HSI) (cf. HEP; Terrell et al. 1982). The p values are not fixed but may vary across the area and habitat types, and if areas are further subdivided into patches with discrete habitat attributes, all p values may vary across patches. Normalization of p values as suitabilities on a 0–1 scale captures the differences among habitat conditions but simplifies calculation and assessment. The maximum productivity rate, or productive capacity, p_{MAX}, is generally assumed to be equal to p_{NOW} values in assessments of permanent physical habitat characteristics. As such, it is the potential of the permanent habitat features that is considered and not its current degraded value arising from load-maintained factors such as eutrophication or acidification. The values of all A and p variables in the equation can be uncertain.

The basic information for a net change analysis can be laid out in a simple format (Table 1). The range of area types represents the basic set of possibilities in development projects changing fish habitat. Loss and modified habitats are those affected by the proposed development. Habitats indirectly affected or only created for compensation purposes are assessed separately. Direct habitats differ from indirect ones as development activities directly modify habitats, whereas changes in water movements may generate indirect changes elsewhere; e.g., construction of a pier may modify longshore sediment transport and produce downstream changes in substrate accumulation and (or) erosion and composition. If an analysis involves multiple habitat patches with varying characteristics, the format can be extended or area-weighted values computed for each area type. The area columns provide a means of checking that areas match where necessary and for reminding the fish habitat management decision maker of the actual areas involved when considering the weighted suitable areas (area × suitability).

Estimates for A variables can generally be obtained by mapping existing habitat conditions at the site of proposed development and overlaying construction information to forecast future habitat conditions. Estimation of indirectly modified areas, MODI, may require some form of hydrodynamic simulation or analysis of expected changes in wave exposure and currents in lakes and oceans or flow rates and turbulence in rivers and streams (W.F. Baird and Associates 1996). Unless the site of proposed development activity is already perceived or known to have highly significant fish productivity, estimates of p variables are generally obtained by inference from observed fish–habitat linkages in other situations using assessments of habitat characteristics at the development site. Detailed site-specific knowledge of fish productivity is the rare exception. Fish–habitat linkages are

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Table 1. Basic template for a net change analysis for fish habitat management where the net change is computed as the difference between post- and pre-development scenarios and summed across area types.

Area type		Predevelopment scenario			Postdevelopment scenario			Net change	
ID	Name	Area (A)	Unit-area PC (p)	WSA (P)	Area (A)	Unit-area PC (p)	WSA (P)	Area (A)	WSA (ΔP)
LOSS	Loss	A_1	p_1	P_1	na	na	na	A_1	$-P_1$
MODD	Modified direct	A_2	p_2	P_2	$A_5 = A_2$	p_5	P_5	A_2	$P_5 - P_2$
MODI	Modified indirect	A_3	p_3	P_3	$A_6 = A_3$	p_6	P_6	A_3	$P_6 - P_3$
COMM	Compensation modified	A_4	p_4	P_4	$A_7 = A_4$	p_7	P_7	A_4	$P_7 - P_4$
COMC	Compensation created	na	na	na	A_8	p_8	P_8	A_8	P_8
TOTAL	Summation	A_{pre}		P_{pre}	A_{post}		P_{post}	A_{sum}	NC

Note: Unit-area PC (p), the unit-area productive capacity metric, usually a suitability index between 0 and 1; WSA (weighted suitable area), the surrogate productivity value, the product of area and unit-area PC ($P = A \cdot p$); na, not applicable; pre, predevelopment, post, postdevelopment; sum, summation; LOSS is absent in the postdevelopment scenario and COMC in the predevelopment scenario.

usually expressed in the form of habitat suitability index (HSI) models based on a variety of empirical observation sources (Terrell et al. 1982).

The uncertainty of unit-area productivity p values is generally expected to be much greater than that of area A values. The terms unit-area productivity (normalized) and suitability are used interchangeably here to describe p values as is usual in fish habitat assessment.

Modelling uncertainty

Based on the review of empirical observations relating fish to habitat presented in the introduction, we decided that a conservative precautionary approach to representing uncertainty about the unit-area productivity (suitability) values for habitat patches was to assume uniform probability distributions. This form of distribution was chosen as it represents both the simplest available for assessing decision-making risk (Morgan and Henrion 1990) and the worst case likely to be encountered. This choice also meant that individual case analyses can be conducted easily using interval analysis (Moore 1979) and that the overall outcome patterns for net change analyses can be assessed using simple Monte Carlo simulations. The approach taken was to examine the overall behaviour of the net change (eq. 1) first using simulation. Then individual examples of habitat management decision making in lakes (case studies) were assessed using interval analysis to develop an operational means of including uncertainty in a net change assessment.

Monte Carlo simulations

Two groups of simulation experiments were done to examine the impact of uncertainty in suitability values in conjunction with the standard set of area types (Table 1), looking at the impacts of uncertainty on the outcome of the weighted suitable area (WSA) net change calculations. The simulation software for these experiments was written using Microsoft's Visual Basic 6, and its intrinsic pseudo-random number generator (PRNG) was used throughout to generate random numbers between zero and one. Prior testing of PRNG did not indicate any measurable bias problems in the generation of random numbers.

The five area types in the net change equation (eq. 1) were employed: area lost (LOSS), area modified directly (MODD), area modified indirectly (MODI), area compensated modified (COMM), and area compensated created (COMC). This was done because all potential net change analyses with more complex, multipatch configurations of habitat can be simplified to the basic form of eq. 1. Net change calculations are such that the combination of these five area types with pre- and post-development scenarios gives eight different habitat patches. Paired patches have the same area but different attributes in pre- versus post-development scenarios (Table 1).

Experiment group 1

In the first group of experiments, the five areas are assumed to be equal and have a value of 100 units (arbitrarily m^2). Five different experiments were done to explore the basic properties of the equation given varying degrees and patterns of uncertainty in the unit-area productivity (p) values, with uncertainty in the area (A) values being ignored. Differences among the randomly generated p values determine the net change result in each trial. In each experiment, 10 000 trials were done in which suitability (p) was allowed to vary randomly, within a uniform distribution, in the range defined for the particular experiment. Each trial simply involved applying random numbers as suitabilities to the areas numbered A1 to A8 in Table 1 and computing the net change (NC) for that drawing:

$$(2) \quad NC_i = p_{i5}A_5 + p_{i6}A_6 + p_{i7}A_7 + p_{i8}A_8 - p_{i1}A_1 - p_{i2}A_2 - p_{i3}A_3 - p_{i4}A_4$$

or

$$(3) \quad NC_i = \sum_{j=5}^{8} p_{ij}A_j - \sum_{j=1}^{4} p_{ij}A_j, \qquad i = 1 \text{ to } 10\,000$$

where, as stated above, A_j are the areas numbered 1 to 8 (Table 1) and p_{ij} are the trial suitabilities, which are varying functions of r_{ij}, the uniformly distributed random numbers on the range 0 to 1. The expected mean p value varied with the experiment.

In reality, there is a possibility that fish habitat patches that are close together will have similar suitability levels or be clustered into groups with more similar within-group suitabilities than between groups. In simulation modelling, such a possibility might be represented by subsets of p values being correlated either positively or negatively. This possibility was

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not examined explicitly in these series of simulations, as it would add considerable complexity to any simulation work. However, the likely impact of such correlations is considered in the analysis of the simulation results.

A series of uncertainty patterns (Fig. 1) for suitability (p) was used in experiments 1*a* through 1*e*. Those patterns are characterized as follows.

(1*a*) Completely random (Fig. 1*a*). As a baseline, the first experiment assumes that we have no knowledge of habitat productivity or suitability and that any p_{ij} value between 0 and 1 may occur (Table 2). The expected mean p is 0.5. This is a worst-case analysis approximating complete ignorance.

(1*b*) Bounded random (Fig. 1*b*). This pattern is similar to that of experiment 1*a* with the expected mean p_{ij} of 0.5 but with the value bounded between narrower bands (Table 2). Such a pattern might arise in nature as a result of fish movements among a larger mosaic of habitat patches populated by sub- or meta-populations in which production dynamics are not spatially synchronized. The movements of the fish could reduce the occurrence of extreme productivity rates. This bounded model provided a basis for assessing the overall effect of narrowing uncertainty bounds; as uncertainty about p values declines, how are net change outcomes influenced?

(1*c*) Wedge random (Fig. 1*c*). This pattern simulates the wedge-pattern phenomenon (Terrell et al. 1996) for relationships for fish-habitat metrics whereby the minimum fish value is always 0 and actual values lie in a distribution between 0 and the maximum value (Table 2). This pattern simulates the situation where habitat conditions supporting lower productivity have a lower range of uncertainty with a zero base compared with habitats supporting higher productivity.

(1*d*) Spread random (Fig. 1*d*). This pattern is a variant of experiment 1*c* in which the minimum value has a proportionality to the maximum value (Table 2), instead of being zero. This approximates the kind of spreading of values often seen in ecological relationships: higher values of the independent variable (habitat metric) have progressively wider ranges of the dependent variable (productivity index) (Cade et al. 1999). This pattern is itself merely a representative of a class of possibilities including nonlinear patterns especially as the range of the habitat metrics is extended. The properties of the simpler curving nonlinearities should be similar to those of the spread random pattern, whereas more complex, possibly discontinuous patterns may be represented by the band patterns described next. The range of uncertainty and the lower boundary value both rise, going from lower to higher productivity habitats.

(1*e*) No band overlap (Fig. 1*e*). This pattern explores the consequence of nonoverlapping categorical assignment of p_{ij} values. It represents a situation where habitats have discrete ranges of productivity or suitability but similar ranges of uncertainty. Two types of simulations were performed (Table 2). In the first (*i*), two nonoverlapping bands with widths of 0.5 were used, and the lower bound was either 0.0 or 0.5. All possible combinations resulting from assigning one of these two bands (low vs. high) to each of the eight areas were tried, and a set of 10 000 net change calculations were done for each combination, resulting in 2^8 or 256 sets of 10 000 net changes. The second type of simulation (*ii*) used three nonoverlapping bands (low vs. medium vs. high) with widths equal to 1/3 and lower bounds of 0, 1/3, and 2/3, resulting in 3^8 or 6561 sets of 10 000 net changes. This allows an assessment of a limited category approach to habitat classification and valuation.

The results for each experiment consisted of the following summary set statistics for the next change variable computed over each set of 10 000 calculations: mean, variance, minimum, maximum, and percent of positive values (PP).

Experiment group 2

The experiments in this group were like those in group 1, except that the areas were not all equal. Each of the experiments in group 1 was repeated 1000 times, each time using a different set of eight randomized areas. Each set of areas was obtained by drawing random numbers and then using the values to scale each of the corresponding areas to between 0 and 100 area units:

$$A_{ij} = 100r_{ij} \quad (4)$$

where A_{ij} is the jth area (j = 1 to 8) in the ith trial (i = 1 to 1000). The areas numbered 5 to 7 (MODD, MODI, and COMM in the postdevelopment scenario) were then set equal to their counterparts (by area type) in the predevelopment scenario. This allowed the effect of differences in area by type to be examined given the uncertainty in suitability values.

Case study assessment using interval analysis

Interval analysis provides a simple basis for assessing individual case studies. Moore (1979) provides an overview of interval calculations. Using the uniform distribution as the simplest representation of the uncertainty associated with suitability values for habitats, the net change equation can be computed using intervals. Instead of expressing p values as fixed points, e.g., as 0.2, 0.55, or 0.7, they are expressed as intervals, e.g., [0.1,0.3], [0,0.5], or [0.4,1.0]. The algebraic properties of interval arithmetic are similar to simple arithmetic with some differences linked to the set properties of intervals (Moore 1979). Interval calculations were done with the RAMAS Risk Calc software of Ferson et al. (1999).

A set of individual case studies was obtained for assessment of uncertainty effects using interval analysis. Bowman et al. (Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 867 Lakeshore Road, Burlington, ON L7R 4A6, unpublished data) undertook a 5-year review of all Fish Habitat Management (Ontario Great Lakes Area, Fish Habitat Management, Fisheries and Oceans, 867 Lakeshore Road, Burlington, ON L7R 4A6) decisions for Great Lakes projects in which in-filling (loss) of nearshore habitat was a key element. A subsample of these projects was subjected to a desk analysis using the defensible methods approach (Minns and Nairn 1999; Minns et al. 2001) to estimate if a net gain or loss occurred. The desk analyses involved extracting area and habitat feature information from available file materials held for each project by Fish Habitat Management in Ontario with no recourse to field observation or measurement (as is the case with most projects subject to decision making). The defensible methods approach uses literature-based ratings of habitat preference or suitability by fish species and life stage for several

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Table 2. Summary of the Monte Carlo simulation designs with the formulae used to estimate p and A values and the settings used in each experiment.

Experiments	Formula	Settings
Experiment 1 (fixed areas)		
(*a*) Complete random	$p_{ij} = a + (b - a)r_{ij}$	a is the lower bound of a band, in this case equal to 0, and b is the upper bound, in this case equal to 1
(*b*) Bounded random	$p_{ij} = a + (1 - 2a)r_{ij}$	a = 0.0, 0.1, 0.2, 0.3, and 0.4 $b = 1 - a$
(*c*) Wedge random	$p_{ij} = b{\cdot}r_{ij}$	a equal to 0 b = 0.1 to 1.0 in increments of 0.1
(*d*) Spread random	$p_{ij} = mb + (b(1 - m))r_{ij}$	$a = m{\cdot}b$ b = 0.1 to 1.0 in increments of 0.1 m = 0.2, 0.4, 0.6, or 0.8
(*e*) No band overlap	$p_{ij} = a_i + (b_j - a_j)r_{ij}$	
(*i*) Two bands		a_i was either 0.0 or 0.5 $b_i - a_i$ was always 0.5
(*ii*) Three bands		a_i was either 0.0, 1/3, or 2/3 $b_j - a_j$ was always 1/3
Experiment 2 (random areas)	$A_{ij} = 100r_{ij}$	
(*a*) to (*e*) repeated	Same as experiment 1	Same as experiment 1

categories of three habitat features: depth, substrate, and vegetation cover. This is the basis for deriving suitability indices for all combinations of habitat categories for groups of species by life stage. Simply stated, combinations of habitat categories preferred by higher numbers of species have higher suitability index values. Seventeen net change analyses were selected from the study (Bowman et al., Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 867 Lakeshore Road, Burlington, ON L7R 4A6, unpublished data) to provide a range of in-fill area sizes, in-fill representing the LOSS component of a net change analysis. Most of these case studies showed a net loss with a fixed-value assessment using defensible methods. Although in several of these case studies there were multiple habitat patches in some area types (e.g., LOSS, MODD, etc.), each case study was summarized using the standard set of area types and composite p values computed (Appendix A).

We evaluated the impact of uncertainty on case study results for three forms of uncertainty: wedge, spread, and categorical (three bands). These forms are considered the most likely to be used to represent uncertainty in an operational fish habitat management context. For the wedge analyses, the fixed-case p values were taken to be the upper bound of the interval, whereas the lower bounds were set to zero. This approach is in keeping with the idea that suitability values obtained using defensible methods represent the highest potential values (Minns et al. 2001). For the spread analyses, lower and upper bounds were set as –50 and +50% of the fixed-case p. For the categorical analyses, the fixed p values were assigned to the interval they overlapped, i.e., low [0,1/3], medium [1/3,2/3], or high [2/3,1]. The final net change interval and the percentage of the final interval exceeding zero (indicating net gain) were used as the indicators. Ahmad (1975) discussed the use of interval analysis in a probability assessment context. In keeping with the scientific convention of seeking a percentage probability as a threshold of significance, the percentage proportion of the distribution exceeding 0 may be considered a proxy probability.

We assessed how increases of newly created habitat for compensation (COMC) might improve the net change when uncertainty was considered. Each case study was modified by adding extra COMC with the same area and unit-area productivity values as those assigned for the LOSS area, simulating implementation of DFO's preferred "like-for-like" compensation strategy. Like-for-like compensation involves matching the habitat characteristics of LOSS areas in COMC areas and, hence, in principle, ensuring NNL. Three levels of extra COMC were used: 1, 2, and 3 × LOSS.

Results

Monte Carlo simulations

Experiment group 1

Although experiments 1*a* to 1*d* differed in how ranges for p were defined, the same range of p was applied to each of the eight areas. Initial inspection of the simulation results showed that simulation results were consistent, as expected, with interval analysis predictions. Empirically, the results were a simple multiplicative function of the bandwidth (BW; the difference between the upper and low bounds of the band, $a - b$ (Table 2, section *a*)), the fixed area size (A), and the combined statistics for the random numbers:

$$(5) \qquad NC_i = A\left(\sum_{j=5}^{8} r_{ij} - \sum_{j=1}^{4} r_{ij}\right) \qquad i = 1 \text{ to } 10\,000$$

The statistics for the quantity within the parentheses were for the actual random numbers used (Table 3). The observed-value coefficients, k_i, were computed from the 10 000 net change values computed in experiment 1*a*. In experiments 1*b*–1*d*, simple arithmetic showed that the expected statistics could be com-

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Table 3. Summary of predictive formulae for the indicator statistics derived from 10 000 net change simulations for experiments 1*a* to 1*d*.

Statistic	Observed value	Expected statistic
Mean	$k_1 = 0.006967$	$k_1 \cdot A \cdot BW$
Variance	$k_2 = 0.682265$	$k_2(A \cdot BW)^2$
Minimum	$k_3 = -2.85427$	$k_3 \cdot A \cdot BW$
Maximum	$k_4 = 2.902881$	$k_4 \cdot A \cdot BW$
% positive (PP)	$k_6 = 50.27$	k_6

Note: k, observed-value coefficient; A, fixed area size; BW, bandwidth.

puted by the formulae given using the k_i values from experiment 1*a*.

The bandwidth is equal to the range for the uniform distribution and varies between and within experiments. In experiment 1*a*, BW = 1 (random); in experiment 1*b*, BW = 0.2 to 0.8 by 0.2 increments (bounded); in experiment 1*c*, BW = 0.1 to 1.0 by 0.1 increments (wedge); and in experiment 1*d*, BW = (0.1 to 1.0 by 0.1 increments) × (0.2 to 0.8 by 0.2 increments) (spread). Thus, experiments 1*a* to 1*d* were all basically the same, as is shown in the predictive formulae (Table 3). The variability was a function of the bandwidth but the percentage outcomes of net gain or loss were constant because the mean suitability in those experiments was set at 0.5. These outcomes are a trivial consequence of the formulations but a necessary backdrop for the parallel experiments with varying areas in experiment group 2.

Despite its apparent complexity, the experiment on categorical bands (1*e*) also yielded results for which means and variances could be computed in advance, in part because only 256 possible unique sets of results were possible for the two-band experiment and 6561 for the three-band case. Another feature was the net sum (NLB) of range lower bounds (LB_j) across area types, so that for any given combination of ranges one has

$$\text{(6)} \qquad \text{NLB} = \left(\sum_{j=5}^{8} \text{LB}_j - \sum_{j=1}^{4} \text{LB}_j \right)$$

and

$$\text{(7)} \qquad \text{Mean} = \text{NLB} \cdot A + (k_1 \cdot A \cdot \text{BW})$$

$$\text{(8)} \qquad \text{Var} = (A \cdot \text{BW})^2 k_2$$

where k_1 and k_2 are statistics for the random number set (Table 3). These formulae worked for all results obtained with experiment 1*e*. The distributions of percentage positive net changes versus NLB for the two- and three-band simulations (Fig. 2) show the transition from predominately negative net changes to predominately positive ones occurs over a very short range of NLB. A four-band scenario was estimated (Fig. 2) using eqs. 7 and 8 showing that the transition becomes more abrupt as the number of bands increases. The curves approximate a cumulative normal distribution and indicate that a 95% probability of net change being greater than zero requires that the NLB be equal to or greater than 2·BW (probability = 99.4%). For one bandwidth, the probability is 88.8%. The result extends to smaller bandwidths. This result indicates that, in the case of equal areas, as long as habitats can be safely assigned to the appropriate band range of suitability, p, there needs to be a minimum either of 2·BW gain in one of the four area pairs (A_5–A_2; A_6–A_3; A_7–A_4; A_8–A_1) and no loss in the other three, or a BW gain in two of the area pairs and no loss in the other two to obtain a net gain with greater than 95% probability.

Increasing the number of bands spanning from 0 to 1 for p is equivalent to increasing the precision of the estimated p. As the assessment of empirical observations indicates that this is an unlikely situation with real data, a habitat classification system with only three or four levels of productive capacity may provide a viable basis for effective decision making.

As mentioned in the previous section, in nature there is the possibility that subsets of the p values will be correlated, i.e., the subsets will be more similar if they are positively correlated and more different if negatively correlated. In general, the more widespread positive correlations are, the less likely the possibility of a net gain. The more similar the p values are between the four area pairs, the less likely a net gain will be obtained. If the p values are more dissimilar between the area pairs, the more likely a net gain if post-development p values are greater than predevelopment p values and vice versa. More complicated patterns of correlation would require additional simulations to determine the shifts in net change outcomes.

Experiment group 2

In the second group of experiments, the areas associated with each area type were allowed to vary between 0 and 100 units. This allowed an exploration of how the relative sizes of different areas, e.g., LOSS, MODI, and COMC, affect the net change outcomes. One thousand randomized sets of areas were created, and for each set of areas, all experiments done in experiment group 1 were repeated. At first glance, this added complexity seemed to rule out the sort of analytical solutions described above, but close examination revealed a great deal of simplification resulting from the mandatory condition that the modified areas A_5, A_6, and A_7 were set equal to A_2, A_3, and A_4, respectively, capturing marginal changes in productive capacity between pre- and post-development. Under these circumstances, the mean net change depends largely on the difference between A_8 and A_1.

In experiment 2*a* (random), the same range (0 to 1), or BW, is used for all eight area types. Thus, for any given area set:

$$\text{(9)} \qquad \text{Mean} = \frac{\sum_{i=1}^{10\,000} \text{NC}_i}{10\,000} = A_2 \sum_i (p_{5i} - p_{2i}) + A_3 \sum_i (p_{6i} - p_{3i}) + A_4 \sum_i (p_{7i} - p_{4i}) + A_8 \sum_i p_{8i} - A_1 \sum_i p_{1i} = A_2(\bar{p}_5 - \bar{p}_2) + A_3(\bar{p}_6 - \bar{p}_3) + A_4(\bar{p}_7 - \bar{p}_4) + A_8\bar{p}_8 - A_1\bar{p}_1$$

Because the mean p values are all equal to 0.5, the effect of the paired differences for areas 2, 3, and 4 is cancelled, leaving the main contrast between areas 8 and 1, COMC and LOSS. The mean was therefore

$$\text{(10)} \qquad \text{Mean} \approx 0.5(A_8 - A_1)$$

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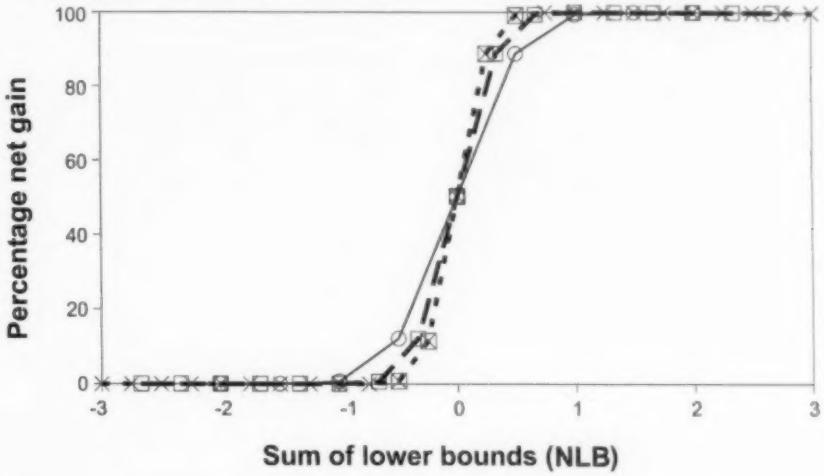
Fig. 2. Plot showing the relationship between the percent positive net change outcomes and the net sum of lower bound values (NLB) (eq. 6) obtained by simulation for the two- and three-band cases (○ and □, respectively) in experiment 1*e* and estimated for the four-band case (×) from eqs. 7 and 8 and the cumulative normal distribution.



It can be similarly shown that the variance could be estimated by extension of the experiment 1*a* result as follows:

$$(11) \quad \text{Var} = \frac{(A_2^2 + A_3^2 + A_4^2)}{6} + \frac{(A_1^2 + A_8^2)}{12}$$

A plot of these observed variances against this computed quantity was 1:1. These results in eqs. 9 to 11 are the same as the additive formulae for area-weighted aggregation of means and variances given a uniform distribution (Yates 1971; Morgan and Henrion 1990). As might be expected from the results for the mean NC, the percent positive (PP) was also strongly related to $A_8 - A_1$ (Fig. 3*a*, BW = 1.0). Thus, in this extreme case where p values are completely random, the net change outcome depends on the difference between loss (LOSS) and created compensation areas (COMC), with the other areas making little difference because any pairwise differences in p are minimal.

In experiment 2*b* (bounded), the same range is again used for all eight area types, but the experiment was repeated five times with ranges centred on 0.5 and BW = 0.2, 0.4, 0.6, 0.8, and 1.0. Means were again a function of $A_8 - A_1$, and again the slope of the line was 0.5, independent of bandwidth. A more generalized equation for estimating variances applies:

$$(12) \quad \text{Var} = \left[\frac{(A_2^2 + A_3^2 + A_4^2)}{6} + \frac{(A_1^2 + A_8^2)}{12}\right]\text{BW}^2$$

Though areas other than A_1 and A_8 do not contribute to the mean, it can be seen that they will have a large effect on the variance as in experiment 2*a*. Again, the percentage of positive net changes (PP) is related to $A_8 - A_1$, the nature of the relationship changing as the bandwidth is reduced, in this example from 1 to 0.4 to 0.2 (Fig. 3). As bandwidth is reduced, the spread becomes much narrower and the transition from loss to gain much more abrupt. This result is consistent with the results obtained in group 1 experiments. All PP values were again predictable given the means and variances.

For experiment 2*c* (wedge), the same range was again used for all eight area types. The experiment was repeated 10 times with ranges bounded below at zero and above at values of 0.1, 0.2, 0.3, etc., up to 1.0. Means could be estimated using the more generalized equation based on the band's midpoint (MID):

$$(13) \quad \text{Mean} = \text{MID}(A_8 - A_1)$$

again a function of $A_8 - A_1$ (COMC vs. LOSS). The same generalized equation for estimating variances applied, and again the predicted means and variances could be used to predict PP very well.

A major difference between the results of this experiment and those of experiment 2*b* is that the appearance of a plot of PP on $A_8 - A_1$ did not appear to depend on BW at all, all plots for all 10 possible bandwidths looking like the plot for BW = 1.0 in experiment 2*b* (Fig. 3*a*). Thus, as the bandwidth was narrowed, there was no tendency to switch abruptly from 100% negative to 100% positive around $A_8 - A_1 = 0$. An explanation of this is that the distribution of PP values versus $A_8 - A_1$ depends on the ratio of MID to BW, which is 0.5 (the minimum possible value) in all cases in experiment 2*c* and in the case in experiment 2*b* only where BW = 1.0.

The MID to BW ratio (MID:BW) is the ratio of quantities related to the parameters defining the underlying distribution of random suitabilities; MID is the mean ($\mu = (a + b)/2$) and BW is proportional to the standard deviation ($\sigma = \text{BW}/\sqrt{12}$) (Morgan and Henrion 1990). Hence, the ratio is a quantity measuring the tightness of that distribution about its mean. The tighter the distribution, the less likely net change will depend on anything other than the difference between A_8 and A_1. The shift into the distribution of percent positive net changes across a range of BW values from experiments 2*a* and 2*b* show this result (Fig. 3) where MID:BW correspond to 1/2, 5/4, and 5/2.

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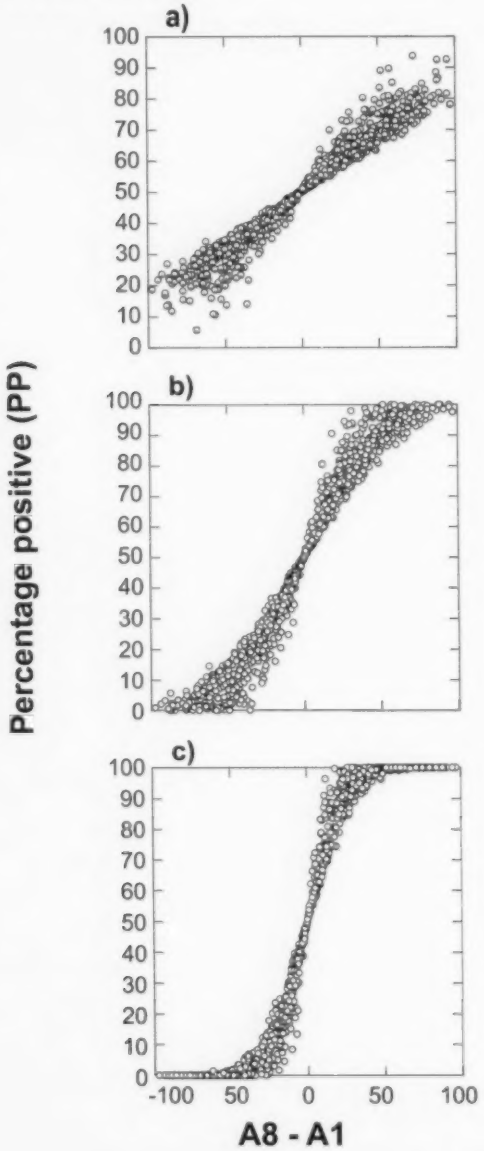
Fig. 3. Plots of percent positive net change (PP), *y* axis, against the difference in area units of the areas for A_8-created compensation (COMC) and A_1 loss (LOSS), *x* axis, for three different bandwidths (BW) from experiments 2*a* and 2*b*: (*a*) BW = 1.0, (*b*) BW = 0.4, and (*c*) BW = 0.2.



Experiment 2*d* (spread) was like experiment 2*c* except that for each of the 10 upper bounds, the experiment was repeated with each of four lower bounds equal to 0.2, 0.4, 0.6, and 0.8 times the upper bound, respectively. The same results with respect to estimated means, variances, and PP applied. Only four possible MID:BW occurred: 6/8, 7/6, 8/4, and 9/2. Several different plots of PP vs. $A_8 - A_1$ were examined, selecting data for different upper and lower bounds. As expected, only four different plots could be detected, corresponding to the four possible MID:BW and similar to the plots shown from experiments 2*a* and 2*b* (Fig. 3). Again, as that ratio increased, the curve shifted progressively toward abruptly switching from 0 to 100% at $A_8 - A_1 = 0$.

In experiment 2*e* (band), nonoverlapping bands were used with bounds depending on area type. In the first instance, BW = 0.5 was used (the two-band case), resulting in 256 possible arrangements of the bands. Because there were 1000 different randomly chosen sets, the result set consisted of 256 000 records. What was expected was that the mean would be predictable from the experimental conditions using a more general form of the equation above:

$$(14)\quad \text{Mean} = (\text{MID}_5 - \text{MID}_2)A_2 + (\text{MID}_6 - \text{MID}_3)A_3 + (\text{MID}_7 - \text{MID}_4)A_4 + \text{MID}_8A_8 - \text{MID}_1A_1$$

The expressions for the predicted variance and PP were expected to be as above (eqs. 12 and 14, respectively). Predicted PP was calculated as

$$(15)\quad \text{PP} = 100(1 - \Pr(x \le 0))$$

where *x* has a normal distribution with mean and variance estimated according to eqs. 12 and 14. Linear regression of predicted on observed values gave results that confirmed expectations (Table 4). This experiment was also done using BW = 1/3 (the three-band case), resulting in 6 561 000 records in the result set. Because of the large size of the result set, physical limitations prevented estimation and confirmation of the percent positive result, but means and variances could be predicted just as above (Table 4).

With the experiment 2*e* trials, an attempt was also made to identify if patterns among the area values (A_1 to A_8) were related to the likelihood of obtaining a positive net change result. A number of indicators based on sums and differences of subsets of the areas were computed, and their correlations with the mean, variance, and percent positive net change values were computed for the two-band case (Table 5). Of the quantities examined, only $A_2 + A_3 + A_4$, $A_1 + A_8$, and $A_8 - A_1$ produced significant correlations. The relationship between the mean and the quantity $A_8 - A_1$ was examined for both the two- and three-band cases (Table 6). The slopes of these regression lines were approximately 0.5 as in experiments 2*a* to 2*d*, but there is much more unexplained variation. The residuals were presumed, based on the effect of bandwidth in other experiments, to be due to variation in suitabilities between pre- and post-development paired areas. It is possible to predict the variance quite well from knowledge of the areas alone (Table 6). The strong relationship between $A_2 + A_3 + A_4$ and the variance indicates that the primary effect of those modified areas and the uncertainties about potential changes in their suitability might be to determine how easy it is to detect a significant net change.

Despite the apparent complexity introduced by randomizing areas by area type in the group 2 experiments, it was still possible in every case to successfully predict the outcome of an experiment for any given area set solely on the basis of the experimental conditions, i.e., the BW and MID of suitabilities defined for each area type. This is expected given that simulations can be done on a case-by-case basis using interval analysis. Many of the regression results represent an approx-

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Table 4. Regression results for observed versus predicted values from eqs. 12, 14, and 15 for the two-band and three-band cases in experiment 2*e*.

Parameter predicted	*r*	Slope	Intercept	*F*
Two-band cases (n = 256 000)				
Mean	1.0000	1.0001	–0.172	7.52×10^{10}
Variance	0.9998	0.9754	3.748	5.65×10^{8}
Percent positive	0.9999	1.0059	–0.433	1.29×10^{9}
Three-band cases (n = 6 156 000)				
Mean	1.0000	1.0001	–0.115	4.98×10^{12}
Variance	0.9998	0.9754	1.667	1.45×10^{10}

Note: Percent positive was not enumerated in the three-band case because the large size of the output exceeded spreadsheet capacity.

Table 5. Correlations between a range of input indicators based on sums and ratios of areas (A) and the performance statistics in experiment 2*e* (two-band case).

	Correlations (n = 256 000) with:		
Quantity	mean	variance	% positive
A_1/A_2	–0.0508	–0.0674	–0.0516
A_1/A_3	–0.0292	–0.0358	–0.0304
A_1/A_4	–0.0311	–0.0528	–0.0306
A_1/A_8	–0.0696	–0.0267	–0.0678
A_2/A_3	–0.0081	–0.0033	–0.0081
A_2/A_4	–0.0003	–0.0560	0.0018
A_2/A_8	–0.0917	–0.0091	–0.0868
A_3/A_4	0.0068	–0.0386	0.0094
A_3/A_8	–0.0967	0.0031	–0.0892
A_4/A_8	–0.0655	–0.0141	–0.0625
$A_8 - A_1$	**0.4459**	–0.0075	**0.4255**
$A_1 + A_8$	–0.0133	**0.3349**	–0.0108
$A_2 + A_3 + A_4$	0.0076	**0.9076**	0.0058
$(A_2 + A_3 + A_4)/A_1$	0.0548	0.0315	0.0453
$(A_2 + A_3 + A_4)/A_8$	–0.0850	–0.0085	–0.0799
$(A_2 + A_3 + A_4)/(A_8 - A_1)$	0.0179	0.0164	0.0171

Note: Bolded numbers are significant values.

imate summary of interval outcomes. Four overall observations can be drawn. (1) As the uncertainty of p, i.e., BW, decreases, there is a sharper transition from net loss to net gain. Given the empirical observations, BW will tend to be wide but a general rule of a net gain of 2·BW across equal areas provides a >95% probability of a net gain. This outcome is equivalent to a compensation ratio of 2:1 for like-for-like habitat compensation, which is the highest preference in DFO's compensation hierarchy. (2) As the midpoint of the range of p (MID) varies, MID:BW determines the level of variability. The MID:BW is equivalent to the inverse of a coefficient of variation. As the ratio increases, the transition from loss to gain becomes sharper. (3) As the proportional contribution of modified areas (MODD, MODI, and COMM) to the total area increases in an assessment, the greater will be the variability as paired uncertainties in p play a greater role in determining the outcomes. This will make it less likely that a net gain or loss can be clearly discerned. (4) The size difference between created compensation (COMC) and loss (LOSS) areas makes the strongest impact on the likelihood of a net gain. This indicates that far more attention should be given to ensuring that losses are balanced by created compensation than to "tweaking" modified areas to secure indiscernible gains.

All that is required to estimate the mean and variance of a population of net change results is the area set (A_1 to A_8), values of MID corresponding to each area type, and BW. In a real-world application, the area set is given by the definition of the problem, an estimate of MID is provided by the suitability computed from the habitat-rating data, and BW is largely unknown though likely large. If one were to assume a particular value for BW and that it did not vary by area type, it is possible to compute percentiles for the distribution of possible net change results using interval analysis.

Many of the simulation results may appear intuitively obvious to many, but it was necessary to confirm the intuition via simulation to safeguard against faulty logic.

Interval analysis of case studies

Most (15/17) of the Great Lakes case studies drawn from Bowman et al. (Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 867 Lakeshore Road, Burlington, ON L7R 4A6, unpublished data) showed a net loss when analyzed using defensible methods (Table 7). The size of in-fill loss varied considerably. In most cases, comparable areas were modified direct (MODD), 6 of 15 involved MODI, 12 involved COMM, and only two involved COMC. The fixed-value calculations performed using defensible methods (Minns et al. 2001) provide a net change result but give no indication of the significance of the result.

The application of three uncertainty patterns is illustrated using case study 17 (Table 8). The suitability (p) and net change in productivity (P) interval values are shown as pairs representing the lower and upper bounds of the uniform distribution within square brackets. For the three modified area types (MODD, MODI, and COMM), the paired differences of p values are computed before being multiplied by the areas and then the net changes are summed across area types. The wedge and categorical uncertainty analyses generate the largest percentage of the distribution greater than zero, 27.2 and 26.8%, respectively, whereas the spread analysis gives only 4.4% (Table 8; Fig. 4). From a scientific perspective, it would be desirable to attain 95% or greater of the distributions being above the NNL point. Further analysis with supplementary created compensation, COMC, based on multiples

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Table 6. Regression results using area indicator variables to predict mean and variance values in experiment 2*e* for both two- and three-band simulations.

Result set	*n*	Coefficients			*r*	*F*
Mean		Constant	$A_8 - A_1$			
Two-band	256 000	0.1729	0.4997		0.4459	6.35×10^4
Three-band	6 561 000	0.1153	0.4998		0.4161	1.37×10^6
Variance		Constant	$A_1 + A_8$	$A_2 + A_3 + A_4$		
Two-band	256 000	−297.44	2.119	4.351	0.9715	2.15×10^6
Three-band	6 561 000	−132.20	0.942	1.934	0.9715	5.52×10^7

Table 7. Summary results of net change analysis for 17 Great Lakes case studies showing the areas (LOSS, MODD + MODI + COMM (modified), and COMC) and the weighted suitable areas (WSA) for the pre- and post-development scenarios and the net change (NC), from Bowman et al. (Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 867 Lakeshore Road, Burlington, ON L7R 4A6, unpublished data) using defensible methods (Minns et al. 2001).

	Areas, m^2			WSA, m^2 equivalents		
Case No.	LOSS	Modified	COMC	Predevelopment	Postdevelopment	NC
1	34 878.0	13 862.0	0.0	20 868.4	2271.7	−18 596.7
2	40.5	17.0	65.1	13.1	19.2	6.1
3	8 000.0	27 925.0	0.0	5 476.0	4607.3	−868.7
4	2 232.5	963.5	0.0	169.0	125.9	−43.1
5	283.7	765.0	487.0	225.7	182.1	−43.6
6	945.0	1 022.0	0.0	267.3	127.7	−139.6
7	284.7	105.3	0.0	116.0	32.0	−84.0
8	240.5	68.0	0.0	28.7	10.5	−18.2
9	85.2	91.6	0.0	57.8	21.7	−36.1
10	28.4	16.0	0.0	15.2	6.5	−8.7
11	34.4	5.6	0.0	11.2	0.6	−10.6
12	29.0	50.9	0.0	30.5	8.6	−21.9
13	255.0	702.0	0.0	458.6	240.0	−218.6
14	170.0	335.0	0.0	15.1	36.2	21.1
15	412.6	592.9	0.0	310.6	93.6	−217.0
16	12.0	94.5	0.0	51.2	40.4	−10.8
17	5 988.0	3 048.8	0.0	1 426.2	533.2	−893.0

of the LOSS component (the same area and unit-area productivity values) shows that much additional compensation is required 50% above the NNL point (case 17 in Table 9). In case 17, added COMC equivalent to 2·LOSS is needed to exceed the 50% point for wedge and spread uncertainty models (60.7 and 71.3%, respectively), whereas 1·LOSS is just sufficient for categorical model (51%). Again, this result is consistent with a concept often proposed among Fish Habitat Management practitioners (C.K. Minns, personal observation) of requiring at least twice as much created compensation compared with any losses to ensure a reasonable expectation of attaining NNL.

The wider analysis of all 17 case studies produced results consistent with the singled-out example (Table 9). The baseline results comparing the three forms of uncertainty produce similar results with the rank order of outcomes being similar. The spread model tends to push results more to extreme values, either low or high, whereas the wedge model produces more homogeneous results. The categorical model makes it much more difficult to attain net gain as compensation is increased. The wedge model is the most representative of the fish–habitat relationships seen in empirical observations; very low or zero fish values are obtained across the whole range of habitat values. When supplementary created compensation is added, it is generally hard to achieve a result of 100% of the distribution above the NNL point. Increasing the compensation area with uncertain suitability values including zero only amplifies the absolute range of potential changes in weighted suitable area. From a more pragmatic habitat manager's perspective, a more reasonable objective might be to have more than 50% of the net change interval distribution exceed zero. Higher values would reflect a more precautionary approach to decision making. For wedge and spread models, 1·LOSS will give results exceeding 50% in nearly half of the cases and 2·LOSS will for all, whereas the categorical bands produce only 17.6% over 50% for 1·LOSS and 94.1% for 2·LOSS. A compromise model between wedge and categorical (three-band model) expressed as three uncertainty classes of [0,1/3], [0.2/3], and [0,1] produces very similar results to the wedge model.

Discussion

Habitat management is assuming a significant role in fisheries resource management (Langton et al. 1996; Auster 2001) as human impacts on all environments intensify. Many habitat

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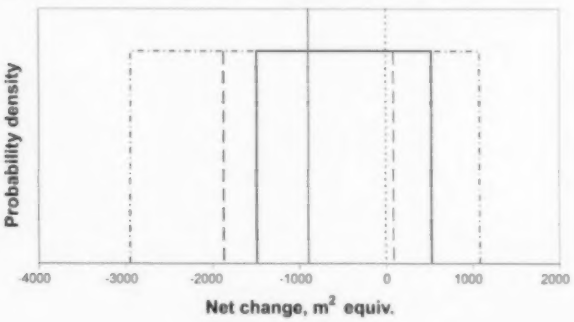
Table 8. Net change analyses for case study 17 showing the results with fixed values and three forms of uncertainty: wedge, spread, and categorical (three band) as described in the text.

Area type	Area *A*	Predevelopment *p*	Postdevelopment *p*	NC ΔP
Fixed				
LOSS	5988.0	0.139	—	–834.2
MODD	1597.0	0.122	0.099	–36.3
MODI	188.0	0.292	0.364	13.6
COMM	1263.8	0.271	0.242	–36.1
COMC	0.0	—	—	—
TOTAL	9036.8			–893.0
Wedge				
LOSS	5988.0	[0,0.139]	—	[–832.2,0]
MODD	1597.0	[0,0.122]	[0,0.099]	[–194.8,158.1]
MODI	188.0	[0,0.292]	[0,0.364]	[–54.9,68.4]
COMM	1263.8	[0,0.271]	[0,0.242]	[–342.5,305.8]
COMC	0.0	—	—	—
TOTAL	9036.8			[–1424.6,532.4]
Spread 0.5				
LOSS	5988.0	[0.0695,0.2085]	—	[–1248.5,–416.2]
MODD	1597.0	[0.061,0.183]	[0.0495,0.1485]	[–213.2,139.7]
MODI	188.0	[0.146,0.438]	[0.182,0.546]	[–48.1,75.2]
COMM	1263.8	[0.1355,0.4065]	[0.121,0.363]	[–360.8,287.5]
COMC	0.0	—	—	—
TOTAL	9036.8			[–1870.6,86.3]
Categorical				
LOSS	5988.0	[0,0.333]	—	[–1994.0,0]
MODD	1597.0	[0,0.333]	[0,0.333]	[–531.8,531.8]
MODI	188.0	[0,0.333]	[0.333,0.667]	[0,125.4]
COMM	1263.8	[0,0.333]	[0,0.333]	[–420.8,420.8]
COMC	0.0	—	—	—
TOTAL	9036.8			[–2946.7,1078.0]

Note: The results show by area type and total: area (m^2) by area type, the value or range of pre- and post-development suitabilities, and the partial and total net change (NC) results in weighted suitable area (m^2 equivalents).

Fig. 4. Results of interval analyses of case study 17 showing the probability distributions for net change of weighted suitable area (WSA) obtained with three different uncertainty models (wedge (solid line), spread (broken line), and categorical (dot–dash line)) in relation to the fixed-value result (solid vertical line) and the no net loss point, zero (vertical dotted line).



management decisions have moderate to high uncertainty, and the potential costs (ecological and economic) indicate the need for a precautionary approach to management (Auster 2001). Unfortunately, in Canada at least, development activities affecting aquatic habitats are often allowed to proceed despite uncertainties about the impacts and the efficacy of many mitigation and compensation actions taken to offset them. Lack of certainty often, perversely, appears to enable a nonprecautionary approach. In Canada, this had tended to foster a subjective, accommodative approach to fish habitat management. Efforts to develop more proactive, objective, science-based approaches are increasing (Minns 2001). As the basic uncertainties in fish–habitat linkages will not be easily reduced, there is a need to incorporate uncertainty as information in decision making (Bradshaw and Borchers 2000). We must make best use of available scientific knowledge and understanding when crafting decision-making procedures for fish habitat as for other natural renewable resources. Morgan and Henrion (1990) have provided 10 commandments for good policy analysis: (1) do your homework with literature, experts, and users; (2) let the problem drive the analysis; (3) make the analysis as simple as possible but no simpler; (4) identify all significant assumptions; (5) be explicit about decision criteria and policy strategies; (6) be explicit about uncertainties; (7) perform systematic sensitivity and uncertainty analysis; (8) iteratively refine the problem statement and analysis; (9) document clearly

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Table 9. Percentage of the resultant net change distribution that is greater than zero for 17 case studies using three forms of uncertainty (wedge, spread, and categorical) for the baseline data and with increments of created compensation (COMC) equivalent to 1, 2, and 3 times the LOSS component.

	Wedge				Spread 0.5				Categorical (three band)			
Case No.	Baseline	COMC + 1	COMC + 2	COMC + 3	Baseline	COMC + 1	COMC + 2	COMC + 3	Baseline	COMC + 1	COMC + 2	COMC + 3
1	9.8	46.1	**61.6**	**70.2**	0.0	42.4	**73.3**	**90.4**	0.0	35.8	**79.0**	100.0
2	**59.5**	68.5	74.2	78.1	**69.0**	86.9	98.4	100.0	**58.8**	68.1	73.9	78.0
3	45.8	**51.7**	56.5	60.4	41.5	**53.4**	63.0	70.8	43.7	50.0	**55.0**	59.1
4	42.7	**59.1**	68.2	74.0	35.4	**68.3**	86.5	98.0	23.2	50.0	**62.9**	70.6
5	44.7	**52.2**	58.0	62.5	39.4	**54.5**	65.9	74.9	**54.4**	59.4	63.4	66.7
6	32.4	47.4	**56.9**	63.5	14.8	44.8	**63.9**	77.1	34.2	50.0	**59.7**	66.2
7	21.6	**50.2**	63.5	71.2	0.0	**50.3**	76.9	92.3	21.3	50.0	**63.4**	71.1
8	26.7	**53.5**	65.9	73.1	3.4	**56.9**	81.8	96.2	18.1	50.0	**64.0**	71.9
9	27.3	46.3	**57.5**	64.8	4.6	42.7	**64.9**	79.5	34.1	50.0	**59.7**	66.3
10	30.0	**51.0**	62.3	69.3	9.9	**51.9**	74.5	88.7	26.5	50.0	**62.1**	69.5
11	5.1	47.7	**63.9**	72.4	0.0	45.3	**77.7**	94.8	12.3	50.0	**65.0**	73.1
12	22.0	39.2	**50.2**	57.9	0.0	28.5	**50.5**	65.7	0.0	18.2	46.1	**66.5**
13	34.6	44.1	**51.3**	56.8	18.7	38.1	**52.6**	63.7	10.7	35.9	**55.2**	70.4
14	70.6	**73.3**	75.6	77.5	**91.1**	96.6	100.0	100.0	39.9	50.0	**57.2**	62.6
15	23.2	42.6	**54.2**	61.9	0.0	35.2	**58.4**	73.8	36.2	50.0	**58.9**	65.1
16	44.1	47.4	**50.4**	53.0	38.2	44.9	**50.8**	56.0	34.1	43.4	**51.8**	59.3
17	27.2	48.9	**60.7**	68.0	4.4	47.9	**71.3**	86.0	26.8	**51.0**	63.2	70.6
Percent > 50%	11.8	47.1	100.0	100.0	11.8	47.1	100.0	100.0	11.8	17.6	94.1	100.0

Note: Those examples where more than 50% of the net change interval exceeds zero are shown in bold. The percentage of case studies where the percentage of the net change distribution exceeds 50% is also shown.

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and completely; and (10) expose the work to peer review. These commandments guided in preparation of this paper and framed the discussion of the results and their implications here.

Commandments 1 to 4 (Morgan and Henrion 1990) have already been addressed above. The literature aspect was outlined in the Introduction. Work on how to implement Canada's fish habitat management policy has gone on for many years with both research and operational components. The exact nature of many fish–habitat linkages remains obscure (Rose 2000) and yet fish habitat managers are faced with the continued need to make decisions. The basic problem faced by Canadian fish habitat managers is how to create an acceptably high probability of attaining NNL. Here we examined how to obtain an acceptable probability of attaining of NNL in the face of uncertainties in fish–habitat relationships. The problem arises in many guises. Scientists have tended to respond to the problem with studies aimed at reducing our ignorance of fish–habitat links and skirted the decision-making issue. However, those decisions must make best use of available science, both empirical evidence and conceptual understanding. The kinds of fish habitat science needed to improve decision making are well known (cf. Minns (2001) for review; Lester et al. 1997; Levings et al. 1997). Interactions with fish habitat managers reviewing projects that affect fish habitat and environmental consultants representing the interests of proponents wishing to carry out projects have been invaluable. Habitat managers will always face uncertainties regardless of the amount of research done and need to begin using techniques like the one described here using interval analysis to explicitly take account of uncertainties when making decisions.

Minns' (1997) net change equation was designed to make the analysis as simple as possible. Here, the approach has been to take the simplest approach to assessing how uncertainty affects net change results. It is unlikely that supplanting the uniform distributions of bandwidths less than one with empirically determined nonuniform uncertainty distributions would significantly affect the conclusions. We have assumed that the areas of habitat affected by development projects can be determined accurately. However, area uncertainty, although relatively less, can be added to an interval analysis. The uniform intervals of suitability values for habitat patches can be estimated from existing knowledge and by experienced professionals in many situations using the wedge, spread, or categorical approaches. Where superior knowledge exists, experienced professionals can use empirical nonuniform uncertainty distributions to describe suitabilities.

For commandment 5, we have developed a robust criterion for successful implementation of the principle of NNL. Given the expected levels of uncertainty, that the conventional scientific criteria of $P = 0.05$ will likely be hard to attain unless substantial compensation ratios (like-for-like COMC : net loss (mostly LOSS)) are mandated. This is an area where we have to cross that science–policy gap (Bradshaw and Borchers 2000). A NNL success threshold of $P > 0.50$ appears attainable and mandates compensation ratios greater than 1 (2 to 3 COMC : net loss with like-for-like created habitat compensation). This rule means that more than 50% of the distribution describing the outcome of a net change analysis taking explicit account of uncertainty must be greater than zero. The case study analyses presented here showed than the $P > 0.50$ criteria would produce improvements over current practice, bringing a precautionary approach closer. The strategy for effective policy implementation should include greater efforts to minimize losses (LOSS) and increase amounts of created compensation (COMC) and relatively less effort on sculpting modified habitats (MODD, MODI, COMM) for questionable gains.

For commandment 6, the uncertainty in fish–habitat relationships is of primary importance in NNL decision making, i.e., the unit-area productivity or suitability values assigned to different patches of fish habitat as a measure of productive capacity. Scientifically those uncertainties are many-fold (Rose 2000). Besides the widespread wedge-shaped phenomena, there are deeper, more challenging questions about the role of physical habitats as limiters of fish productivity, including life-stage bottlenecks (Minns et al. 1996*a*, 1996*b*). Nutrient levels and biotic interactions doubtlessly play a role in determining both total fish productivity and its allocation among species and stocks. Despite these uncertainties, many fish habitat managers and development proponents routinely claim to be able to identify limiting habitat factors, and thereby to be able to priorize losses, and mitigation and compensation actions. Here we have focused on the first layer of uncertainty, taking an approach that will be precautionary when applied. The uniform probability distribution provides a simple, worst-case expression of the fish-habitat uncertainties and facilitates a practical approach to using uncertainty in decision making.

For commandment 7, the case study results are consistent with the results obtained in the Monte Carlo simulation modelling and further demonstrate the dominance of the LOSS and COMC components in net change analyses. Suitability (p) changes in modified habitats (MODD, MODI, and COMM) increase the variation, making it more difficult to obtain a clear NNL threshold. The simulation results indicated that there might be a minimum 2:1 ratio of created compensation to loss habitats with similar productivities required to gain a high certainty of NNL. The case studies also reinforced the simulation results on the need for greater levels of compensation to offset losses. The empirical evidence favours the wedge model of uncertainty and hence is recommended as the first choice for any consideration of uncertainty in NNL calculations. If there is a basis for estimating the upper bound values of wedge uncertainty distributions from empirical data, it can be done, although a combined wedge–categorical approach will yield similar results where the upper bounds may be obtained by consensus.

Commandments 8 to 10 have also been addressed through the many design iterations involved in the development of approaches like defensible methods (Minns et al. 2001) and HEP (Terrell et al. 1982) and in this paper. The basic framework for assessing net change has been reported (Minns 1997) and an example application tool for lake fish habitat based on it documented (Minns and Nairn 1999; Minns et al. 2001). In this paper, the simulations to examine the overall behaviour of the net change equation with uncertainty added have been described along with the case study analyses using interval analysis. The next step involves the implementation of an uncertainty analysis software application with an accompanying guideline document for use by fish habitat managers and others.

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The results obtained both in simulation and case studies combined with extant empirical knowledge of fish–habitat relationships point to some key conclusions and recommendations for the conduct of fish habitat management in the context of Canada's Fisheries Act and its habitat policy (viz. NNL).

Conclusions

(1) Uncertainty can be incorporated in decision making based on assessment of net gain or loss of productive capacity. (2) Despite the broad uncertainty surrounding many fish–habitat relationships, simple habitat classifications involving as few as three or four levels of productive capacity can provide a basis for robust decisions. (3) The loss and created compensation elements of a NNL assessment should garner the most attention through minimizing loss and maximizing offset-created compensation, as minor shifts in modified habitats (direct, indirect, or compensation) have a marginal affect on NNL outcomes. (4) All results here point to a valid basis for requiring at least twice the level of created compensation for any losses on a like-for-like basis over a broad range of uncertainty.

Recommendations

(1) NNL assessment of fish habitat should include explicit consideration of the uncertainties, using simple habitat classifications involving few levels of productive capacity. (2) NNL assessments should employ a wedge-shaped uncertainty model, which can be superseded when empirical characterization of the uncertainty distribution is available. (3) A minimum compensation requirement of a 2:1 ratio of areas of habitat creation to loss be established with created habitat having the same characteristics as the loss habitat (like-for-like) until the uncertainties association with measuring the productive capacity of existing and created habitats be greatly reduced from current levels.

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(Appendix A next page.)

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Appendix A

Table A1. Area (A) and unit-area productivity/suitability values (p) for 17 case studies assessed in the Great Lakes from Bowman et al. (Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 867 Lakeshore Road, Burlington, ON L7R 4A6, unpublished data) using defensible methods (Minns et al. 2001).

	Areas (m^2)					Unit-area productivity/suitability values							
Case No.	LOSS, A_1	MODD, A_2/A_5	MODI, A_3/A_6	COMM, A_4/A_7	COMC, A_8	p_1	p_2	p_3	p_4	p_5	p_6	p_7	p_8
1	34 878.0	3555.0	33.0	10 274.0	0.0	0.448	0.385	0.364	0.375	0.104	0.330	0.184	0.000
2	40.5	0.0	0.0	17.0	65.1	0.227	0.000	0.000	0.229	0.000	0.000	0.253	0.229
3	8 000.0	1500.0	0.0	26 425.0	0.0	0.155	0.087	0.000	0.155	0.046	0.000	0.172	0.000
4	2 232.4	647.1	0.0	316.4	0.0	0.053	0.053	0.000	0.051	0.107	0.000	0.179	0.000
5	283.7	456.2	308.8	0.0	487.0	0.227	0.210	0.212	0.000	0.096	0.212	0.000	0.150
6	945.0	1022.0	0.0	0.0	0.0	0.119	0.151	0.000	0.000	0.125	0.000	0.000	0.000
7	284.7	105.3	0.0	0.0	0.0	0.298	0.297	0.000	0.000	0.304	0.000	0.000	0.000
8	240.5	20.0	0.0	48.0	0.0	0.094	0.090	0.000	0.092	0.105	0.000	0.175	0.000
9	85.2	31.6	0.0	60.0	0.0	0.331	0.307	0.000	0.332	0.108	0.000	0.305	0.000
10	28.4	0.0	0.0	16.0	0.0	0.327	0.000	0.000	0.369	0.000	0.000	0.406	0.000
11	34.4	5.6	0.0	0.0	0.0	0.279	0.286	0.000	0.000	0.107	0.000	0.000	0.000
12	29.0	11.5	0.0	39.4	0.0	0.383	0.383	0.000	0.381	0.104	0.000	0.188	0.000
13	255.0	270.0	432.0	0.0	0.0	0.476	0.460	0.493	0.000	0.100	0.493	0.000	0.000
14	170.0	262.0	0.0	73.0	0.0	0.031	0.031	0.000	0.023	0.105	0.000	0.118	0.000
15	454.0	310.5	111.4	171.0	0.0	0.302	0.291	0.302	0.289	0.107	0.302	0.156	0.000
16	12.0	0.0	80.5	14.0	0.0	0.483	0.000	0.481	0.479	0.000	0.481	0.121	0.000
17	5 988.0	1597.0	188.0	1263.8	0.0	0.139	0.122	0.292	0.271	0.099	0.364	0.242	0.000

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Requests for permission to republish the paper, in whole or in part, should be sent to NRC Research Press.

Preparation of manuscripts

General guidelines

Movement of manuscripts through review channels and the Editorial Office is greatly expedited if manuscripts are prepared in Journal style and format. General guidelines follow.

Type the manuscript on white paper (21.6 × 27.9 cm (8.5 × 11 in.)) on only one side of the page. Leave all margins at least 2.5 cm (1 in.) wide. Type only the title, authors' names and affiliations, and related footnotes on the first page. Number all pages beginning with the title page, including those for tables and captions for illustrations. **Double-space all parts of the manuscript**, including tables, captions for tables and figures, footnotes, and the reference list. Use italic font on for material that is to be set in italics. Do not use all capitals anywhere in the manuscript. Use the name-and-year system for literature citations.

Editorial practices

Spelling should follow that of *Webster's Third New International Dictionary* or the *Oxford English Dictionary*. Authors are responsible for consistency in spelling.

The *CBE Manual for Authors, Editors, and Publishers: Scientific Style and Format* (6th ed., 1994) published by the Council of Biology Editors, Inc., Chicago, IL 60603, U.S.A., is used as the authority in matters of form. Titles of periodicals are abbreviated as in *BIOSIS® Serial Sources* (BIOSIS, 2100 Arch Street, Philadelphia, PA 19103-1399, U.S.A.). Authors are responsible for ensuring the accuracy and completeness of their reference list. The Journal follows the names and spelling for fishes recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (5th ed., 1991, Spec. Publ. No. 20, American Fisheries Society) and the gene nomenclature for protein-coding loci outlined in Shaklee et al. (1990, Trans. Am. Fish. Soc. **119**: 2–15). **SI** units (Système international d'unités) should be used or SI equivalents should be given. This system is explained and other useful information is given in the *Metric Practice Guide* (2002) published by CSA International (178 Rexdale Blvd., Toronto, ON M9W 1R3, Canada). For practical reasons, some exceptions to SI units are allowed (noted in the editorial in the Journal, Vol. 40, No. 12).

Checklist for manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed and organized to facilitate comparison? Are there inconsistencies between tables and figures and the text, or within the text? Should some of the data be made available separately in a data or manuscript report or at a data depository?

If statistical analysis is included, is it subordinate to the research? When probability statements are made, are only the statistical tests cited and unnecessary statistical tables excluded?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the **title** encompass the content of the report? Does the **Abstract** give the essentials of the new knowledge? Is the **Introduction** largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of **Materials and methods** limited to what readers need to understand the design of the study and to judge the adequacy of the data? Are generalizations from the **Results** supported by the data provided? Are findings distinguished from inferences? Is the **Discussion** limited to interpretation and significance of the findings?

The most common technical problems in submitted manuscripts are listed below. Authors can hasten the processing of

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their papers if they pay attention to these points during manuscript preparation.

(1) Limit the abstract to one paragraph of about 175 words.
(2) Double-space all elements of the manuscript, including references, table captions, and figure legends.
(3) Avoid exclusive use of capitals anywhere in the manuscript, including headings, table captions, and figure legends.
(4) Italicize only Latin names of organisms and appropriate statistical and mathematical notations.
(5) Use correct SI symbols for units or measure in figures, tables, and text. Place a zero before the decimal for numbers less than unity.
(6) Avoid ambiguous forms such as g $C/m^2/day$; use g $C \cdot m^{-2} \cdot day^{-1}$.
(7) Identify the test used to test statistical significance and give the probability value. No reference is needed for common statistical tests.
(8) In the text, generalize from tables and figures; avoid repeating all of the details. Be sure each table and figure can stand on its own and is referred to in the text in numerical order. The captions should explain the purpose of the table or figure.
(9) Include an acknowledgement section at manuscript stage, not when page proofs arrive.
(10) Provide the person's initials and mailing address when referring to personal communications.
(11) Delete unnecessary references that do not apply directly to the problem.
(12) Check references carefully against text citations and vice versa to ensure exact correspondence. Provide an availability statement for less easily retrieved material, e.g., available from Department of Economics, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.
(13) Delete commas between name and date in citations such as (Smith 1990) and do not underline or italicize "et al.".
(14) Photocopies of figures, except halftones, are appropriate for review purposes. Send photographic prints, laser printouts, or original artwork/electronic files of figures (see "Illustrations" and "Preparation of electronic illustration files") on request for publication. Use the same type of lettering throughout if possible.

Parts of the manuscript

Organization

Organize the manuscript on the basis of the purpose or scope of the study as stated in the introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations first is one of the most prominent shortcomings in presentation of manuscripts.

Make certain that everything in each section is relevant to the heading and that everything in each paragraph is relevant to the topic (opening) sentence.

Before writing any paragraphs, try writing the topic sentences for all of them and arranging these in appropriate order.

Title

Limit the title to what is documented in the manuscript. It is the key to the article and should clearly and concisely reveal what appears in the paper itself. The title serves two functions: (1) it allows the reader to judge whether or not the article is of potential interest and (2) it should provide enough information to permit the reader to judge the scope and potential importance of the article. Words in the title should convey a maximal amount of information and identify the nature of the research, organism used, and where appropriate, the technical approach (e.g., X ray, chromatography, mathematical analysis). Titles should not begin with a numeral or introductory prepositions such as "On" or "Towards" or expressions such as "A contribution to..." or "Investigations on...". Good titles greatly assist scientists and librarians in using scientific literature and aid indexers in preparing titles for keyword indexes. Series titles should be avoided.

Abstract

An abstract is required for all manuscripts and should state concisely, in up to 175 words, what was done, found, and concluded. Authors who can submit abstracts in both fluent English and fluent French are encouraged to do so.

Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article. Begin the abstract with the main conclusion from the study, and support it with the relevant findings. Limit details of methods to those needed in understanding what was done, and work them into statements of findings. Avoid using phrases such as "...is discussed" or "...was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents and be completely self-contained (i.e., any *essential* references) in a retrievable form (e.g., R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. **37**: 268–282).

Introduction

Limit the introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and adding guideposts to orient the reader. An introduction generally need not exceed 375–500 words.

Materials and methods

Materials and methods provides the framework for getting answers to the questions posed in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all the information in one section when

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possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine...we...". If the section is long, consider using subheadings corresponding to headings for the findings.

Results

Limit the results to answers to the questions posed in the purpose of the work, and condense them as comprehensively as possible. Give the findings as nearly as possible in the terms in which the observations or measurements were made so as to avoid confusion between facts and inferences. State noteworthy findings to be noted in each table and figure, and avoid restating in the text what is clear from the captions. Material supplementary to the text can be archived in the report literature or a recognized data depository and referenced in the text.

Discussion

Limit the discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Emphasis should be maintained on synthesis and interpretation and exposition of broadly applicable generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the discussion with a short summary of the significance of the work and conclusions drawn. If the discussion is brief and straightforward, it can be combined with the results section.

Acknowledgements

We strongly urge authors to limit acknowledgments to those who contributed substantially to scientific and technical aspects of the paper, gave financial support, or improved the quality of the presentation. Avoid acknowledging those whose contribution was clerical only.

References

References should be selected judiciously and be largely restricted to significant, published literature. References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings may not be cited in the reference list but may be noted in the text as unpublished data or personal communications (include mailing addresses). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. **Citations of literature in the text should be carefully checked against those in the reference list and vice versa to ensure exact correspondence.** Nearly every manuscript submitted to the Journal contains errors in the references.

Footnotes

Footnotes to material in the text should not be used unless they are unavoidable, but their use is encouraged in tables. Where used in the text, footnotes should be cited in the manuscript by superscript Arabic numbers (except in the tables, see below) and should be numbered serially beginning with any that appear on the title page. Each footnote should be typed on the manuscript page on which the reference to it is made; **footnotes should not be included in the list of references**.

Equations

Equations should be clearly typed; triple-spacing should be used if superscripts and (or) subscripts are involved. Superscripts and subscripts should be legible and carefully placed. Distinguish between lowercase *l* and the numeral *one*, and between capital *O* and the numeral *zero*. A letter or symbol should represent only one entity and be used consistently throughout the paper. Each variable must be defined in the text or in a **List of symbols** to appear after the reference list. Variables representing vectors, matrices, vector matrices, and tensors must be clearly identified. Numbers identifying equations must be in parentheses and placed flush with the **left margin**. In numbering, no distinction is made between mathematical and chemical equations.

Tables

Tables are used to present repetitive data and should be as economical of space as possible. Design tables to fit a one- or two-column width of the Journal. Type each on a separate page and number with Arabic numerals. Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra space instead. Table captions should be succinct and identify the purpose of the table sufficiently well to allow the table to stand on its own. Indicate table footnotes by superscript lowercase letters and type them below the table. Place the tables after the list of references. Note that *text tables* are not numbered, are typed within the text, and seldom need horizontal lines.

Appendices

Appendices should be indicated sequentially by A, B, C, etc., and figures and tables in the appendices should be numbered separately from those used in the main body of the paper, for example, Fig. A1, Table A1, etc.

Supplementary material

The National Research Council of Canada maintains a depository in which supplementary material may be placed, at either the request of the author or the suggestion of the Senior Editor. In addition, supplementary material can now be made available in its native file format on the Journal Web site. It will be linked from the Web page of the associated article. Such material may include extensive tables of data, detailed calculations, and maps not essential for understanding and evaluating the paper. Such material must be clearly marked when the manuscript is submitted. Tables and figures should be numbered in sequence separate from those published with the paper (e.g., Fig. D1, Table D1). The supplemental material should be referred to by footnotes. Copies of material in the depository may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

Illustrations

Provide photographic reproductions, laser printouts, or the original artwork (no larger than 27.9 × 43.2 cm (11 × 17 in.)) of each illustration. Provide three sets of illustrations for review purposes.

Each figure or group of figures should be planned to fit, after appropriate reduction, into the area of either one or two columns of text. The maximum finished size of a one-column illustration is 8.8 × 23.9 cm (3.5 × 9.4 in.) and that of a two-column illustration is 18.2 × 23.9 cm (7.2 × 9.4 in.). The figures (including halftones) must be numbered consecutively in Arabic numerals, and each one must be referred to in the text and must be self-explanatory. All terms, abbreviations, and symbols must correspond with those in the text. Only essential labelling should be used, with detailed information given in the

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caption. Each illustration must be identified by the figure number and the authors' names on the back of the page or in the left-hand corner, well away from the illustration area.

Line drawings should be made with black ink or computer-generated in black on high-quality white paper or other comparable material. For computer-generated graphics, supply a laser print at the highest resolution available. **Photocopies are not acceptable.**

All lines must be sufficiently thick (0.5 points minimum) to reproduce well, and all symbols, superscripts, subscripts, and decimal points must be in good proportion to the rest of the drawing and large enough to allow for any necessary reduction without loss of detail. Avoid small open symbols; these tend to fill in upon reproduction. **Lettering produced by dot matrix printers or typewriters, or by hand, is not acceptable.** The same font style and lettering sizes should be used for all figures of similar size in any one paper.

Maps must have very clear, bold patterns and must show longitudes and latitudes (or UTM coordinates) and a scale. On **maps of Quebec**, the official name of municipalities must be used (e.g., Québec, Montréal, and Clarke City) and physical features must be in French (e.g., Lac Bienville) except for those that are considered of pan-Canadian significance. Areas of pan-Canadian significance have an official form in English and French (e.g., Atlantic Ocean and océan Atlantique) and should appear in the language of the paper. Quebec (the province) must also appear in the language of the paper. For a complete list of names of areas of pan-Canadian significance, see pp. 236-237 of Le guide du rédacteur (2nd ed., 1996), published by Public Works and Government Services Canada, Ottawa, ON K1A 0S5.

Photographs should be *continuous tone* on glossy paper. Prints must be of high quality, on glossy paper, with strong contrast. The copies for reproduction should only show essential features, be trimmed, and mounted on **thin** flexible white bristol board with no space between those arranged in groups. A photograph, or group of them, should be planned to fit into the area of either one or two columns of text **with no further reduction**. Electron micrographs or photomicrographs should include a scale bar directly on the print. The best results will be obtained if the authors match the contrast and density of all figures arranged as a single plate.

Color illustrations will be at the author's expense. Further details on prices are available from Cecily Pearson, Managing Editor of the Journal (613-993-9099; fax: 613-952-7656; e-mail: cecily.pearson@nrc.ca).

NRC Research Press prefers the submission of electronic illustration files for accepted manuscripts and will use these electronic files whenever possible. If electronic files are not available, paper versions of the figures will be scanned. Note that the scanner will easily reproduce flaws (e.g., correction fluid, smudges). Submission of noncontinuous (screened) photographs and scanned illustrations printed out on laser printers is not recommended as moirés develop; a moiré is a noticeable, unwanted pattern generated by rescanning or rescreening an illustration that already contains a dot pattern.

Preparation of electronic illustration files

Authors must supply electronic graphic files and **high-quality, hard-copy originals. Electronic files (i.e., figure number and figure content) should match the originals.** On the disk label, identify (1) the software application and version and (2) file name(s), size, and extension. If you have compressed your files, indicate what compression format was used. PC or Macintosh versions of True Type or Type 1 fonts should be used. **Do not use bitmap or nonstandard fonts.** Electronic graphics can be accepted on the following disks: 3.5-in. disks, 100-MB Zip cartridge, and CD-ROM.

The preferred graphic application of NRC Research Press is CorelDraw! For other applications that can be used, see the "Electronic graphics list" at http://pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_prog_e?cjfas_graphics_e.html.

All figures should be submitted at their final published size. For figures with several parts (e.g., *a*, *b*, *c*, *d*, etc.) created using the same software application, assemble them into one file rather than sending several files.

Remember that the more complex your artwork becomes, the greater the possibility for problems at output time. Avoid complicated textures and shadings, especially in vector illustration programs; this increases the chance for a poor-quality final product.

Bitmap (raster) files — Bitmaps are image files produced using a grid format in which each square (or pixel) is set to one level of black, colour, or grey. A bitmap (rasterized) file is broken down into the number of pixels or picture elements per inch (ppi). Pixels per inch is sometimes referred to as dots per inch (dpi). The higher the resolution of an image, the larger the number of pixels contained within the rectangular grid.

The proper resolution should be used when submitting bitmap artwork. The minimum requirements for resolution are 600 dpi for line art and finelines (line art with fine lines or shading), 300 dpi for halftones and colour, and 600 dpi for combinations (halftones with lettering outside the photo area).

All *colour* files submitted must be as CMYK (cyan, magenta, yellow, and black). These colours are used in full-colour commerical printing. RGB graphics (red, green, and blue; colours specifically used to produce an image on a monitor) will not print correctly.

Vector files — Vector files are image files produced using elements such as lines and shapes. Typically these files are used for *line drawings*.

Bitmaps inside vector files — Bitmaps can be imported into vector/draw applications only for the purpose of adding and overlaying information, lines, text, etc. Bitmaps should not be resized, cropped, rotated, or otherwise manipulated after importing.

Format conventions

Abbreviations

Abbreviate terms denoting units of weight and measurement in the text only when they are preceded by numerals.

becquerel (Bq)
calorie (cal)
centimetre (cm)
centimetre, square (cm^2)
centimetre, cubic (cm^3)
centimetres per gram per second ($cm \cdot g^{-1} \cdot s^{-1}$)
coulomb (C)
decimetre (dm)
degree Celcius (°C)
degrees of freedom (df)
gram (g)
hectare (ha)
hertz (Hz)
hour (h)
joule (J)
kilometre (km)
litre (L)
lumen (lm)
lux (lx)
metre (m)
metre, square (m^2)
metre, cubic (m^3)
micrometre (µm)
milligram (mg)
millilitre (mL)
millimetre (mm)

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millimetre, square (mm^2)
minute (min)
molar mass (M)
mole (mol)
moles per litre (mol/L, M)
Pascal (Pa)
second (s)
standard deviation (SD)
standard error (SE)
tonne (metric ton) (t)
volt (V)
volume (vol)
watt (W)

Dates

Dates should be written in the sequence day–month–year without internal punctuation (On 9 October 1983 the...).

Reference citations in text

Name-and-year system

The Journal uses the name-and-year system of citation; that is, the surname of the author(s) and the year of publication are inserted in the text at an appropriate point: "Brown (1983) compared..." or "...were compared (Brown 1983)". If the reference has more than two authors, include only the surname of the first author followed by "et al." (not italicized): "Brown et al. (1983) compared..." or "...were compared (Brown et al. 1983)".

Personal communications

Personal communications are not listed in the reference list. Using parentheses in the text, state the name and mailing address of the communicator followed by "personal communication".

Unpublished data

If an unpublished book or article has been accepted for publication, list it in the reference list section followed by the notation "In press". Only those manuscripts that are in galley or page proof stage or for which there is an acceptance letter can be considered in press. If an article is submitted but not yet accepted, state the name and address of the author of the unpublished material followed by the notation "unpublished data" in the text and do not include it in the reference list.

Reference lists

References should be listed at the end of the paper in alphabetical order according to surnames of the first author. References with the same first author are listed in the following order. (1) Papers with **one author only** are listed first in chronological order, beginning with the earliest paper. (2) Papers with **dual authorship** follow and are listed in alphabetical order by the last name of the second author. (3) Papers with **three or more authors** appear after the dual-authored papers and are arranged chronologically.

The following bibliographic citations illustrate the punctuation, style, and abbreviations (according to *CASSI* or *BIOSIS® Serial Sources*) for references.

Journal article

Peterman, R.M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. **39**: 1444–1452.

Entire issue of journal

Gordon, D.C., Jr., and Hourston, A.S. (*Editors*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40**(Suppl. 1).

Book in a series

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Book not in a series

LeBlond, P.H., and Mysak, L.A. 1978. Waves in the ocean. Elsevier, New York.

Part of book

Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, Britsh Columbia. *In* Salmonid ecosystems of the North Pacific. *Edited by* W.J. Neil and D.C. Himsworth. Oregon State University Press, Corvallis, Oreg. pp. 203–229.

Corporate author

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, D.C.

Theses

Kutty, M.N. 1999. Some studies on the respiratory quotient in goldfish and rainbow trout. Ph.D. thesis, University of Toronto, Toronto, Ont. Natl. Libr. Can., Can. Theses Microfilm No. 646.

Reports

Smith, J.E. 1981. Catch and efforts statistics of the Canadian groundfish fishery on the Pacific coast in 1980. Can. Tech. Rep. Fish. Aquat. Sci. No. 1032.

Translation

Koike, A., and Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64**: 1–11. [Translated from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983.]

Word list

The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the Journal's house style for these commonly used terms:

age-class (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)

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saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

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Recommandations aux auteurs

Journal canadien des sciences halieutiques et aquatiques

La Rédaction encourage la soumission d'articles contribuant à l'enrichissement des connaissances des sciences halieutiques et aquatiques. Les articles peuvent porter sur les cellules, les organismes, les populations, les communautés, les écosystèmes ou les procédés qui affectent les systèmes aquatiques. Ils peuvent traiter de disciplines variées y compris la biologie et l'écologie des organismes d'eau douce et d'eau salée, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, les maladies et la gestion. Les articles sont choisis selon la portée et l'importance des nouvelles connaissances ou idées qu'ils contiennent. On accorde la préséance aux articles qui contribuent à la compréhension de phénomènes observés et à l'interprétation de résultats expérimentaux.

Nous invitons les auteurs à soumettre des articles ayant des objectifs précis ou relevant des hypothèses, concepts ou questions vérifiables et se terminant par de solides conclusions ou d'utiles synthèses. Ces articles enrichissent, changent, mettent en question ou réorientent les connaissances acquises sur divers aspects des sciences aquatiques. **La raison d'être de l'analyse et l'interprétation des résultats doivent être situées dans un vaste contexte disciplinaire ou interdisciplinaire.** Les articles de méthodologie et de modélisation doivent inclure des applications et prouver la supériorité de la méthodologie ou du modèle explicité.

La Rédaction décourage la soumission d'articles simplement descriptifs (à moins qu'il ne s'agisse de nouvelles disciplines), d'application très limitée (applicable à une seule année, une seule région ou un seul taxon, portant sur un unique composé chimique, etc.); d'articles qui ne font que reprendre les principes énoncés dans des articles précédents; et d'articles rendant compte de l'application de normes sans gain de méthodologie. Les études préliminaires ou fragmentaires, ou dont la pertinence à grande échelle n'est pas démontrée, et les interprétations purement spéculatives sont carrément rejetées.

Les articles doivent être aussi complets que possible. S'il est impossible d'inclure toute les données pertinentes dans un seul article, l'auteur devra inclure des renvois à des articles connexes et soumettre ceux-ci avec son propre article.

Le Journal publie le genre de textes suivants :

Articles — Études de vaste portée qui constituent de nouvelles contributions à la science.

Perspectives — Synthèses, synthèses critiques ou réévaluations de concepts ou de paradigmes couramment admis.

Discussions — Commentaire ou réponse sur des sujets récemment abordés dans le Journal.

Communications rapides — Présentations de nouveaux concepts, descriptions de nouvelles méthodologies ou courts textes sur des sujets d'actualité ou controversés.

On peut obtenir les caractéristiques précises de chacun de ces genres sur le site Web du Bureau de la rédaction http://www.uoguelph.ca/~cjfas/.

Processus de publication

La Rédaction **encourage les auteurs à soumettre leurs manuscrits par courriel** à cjfas@uoguelph.ca en format Word, WordPerfect ou PDF. Pour obtenir de plus amples renseignements sur la soumission électronique, y compris les formats de fichier acceptés, communiquez directement avec la Rédaction.

Si vous **optez pour la soumission par courrier**, vous devez soumettre les manuscrits (**en triple**) à la directrice scientifique principale, *Journal canadien des sciences halieutiques et aquatiques*, University of Guelph, Département de zoologie, édifice 006, bureau 107, Guelph, ON N1G 2W1, Canada. Veuillez inclure le texte, les tableaux et les figures du manuscrit sur disquette, en précisant le(s) progiciel(s) et la (les) version(s) utilisés; le logiciel de traitement de textes préférés est Microsoft Word pour **l'examen par les réviseurs**. **Les manuscrits et les illustrations doivent être solidement emballés afin d'être protégés lors de l'expédition.**

Nous encourageons la soumission d'articles brefs, de style clair. Nous accepterons d'examiner les manuscrits plus longs si leur importance et leur interprétation de nouvelles connaissances en justifient la longueur.

Tous les manuscrits doivent être accompagnés d'une lettre qui fait état (1) des principaux points et de l'importance du travail, (2) de la participation de tous les auteurs au manuscrit et de leur approbation de ce dernier, (3) de l'assurance que le manuscrit en question n'est pas en cours d'examen aux fins de publication dans une autre revue, (4) de suggestions quant aux arbitres éventuels, (5) d'autres manuscrits, y compris de résumés détaillés, contenant une information identique ou similaire à celle contenue dans le manuscrit soumis et (6) des numéros de téléphone et de télécopieur ainsi que du courriel et de l'adresse de chaque auteur. L'auteur devra, de préférence, conserver les originaux du texte dactylographié et des figures (sauf les demi-teintes) jusqu'à ce qu'on les lui demande.

La directrice scientifique principale reconnaît la possibilité que des conflits d'intérêts réels ou perçus surviennent à la suite de circonstances intellectuelles, personnelles ou financières liées aux travaux de recherche. Or, les manuscrits devraient inclure une divulgation de toute source de financement de la recherche. De plus, la lettre de transmission devrait comprendre une explication de tout conflit d'intérêts, réel ou perçu, qui pourrait survenir lors du processus d'examen par les pairs. Si de tels conflits ne sont pas divulgués, le manuscrit pourrait être refusé.

Chaque article est habituellement soumis à une évaluation par au moins deux réviseurs. Toutefois, la directrice scientifique principale renverra sans les évaluer tout article qui ne reflète pas la portée ou le caractère du Journal et les articles qui débordent des limites imposées pour la publication sous forme de « résumés approfondis ». On obtiendra les directives à cet égard sur le site Web du Bureau de la rédaction. Les articles soumis aux fins de publication dans un supplément sont soumis au même rigoureux exercice d'examen que les articles des numéros réguliers.

On demande habituellement aux auteurs d'examiner les commentaires des réviseurs et de modifier leur texte en conséquence en 90 jours, tout au plus. Faute de respecter ce délai, l'article renvoyé par l'auteur sera traité comme une nouvelle soumission à moins que l'auteur n'ait au préalable dûment communiqué avec le Bureau de la rédaction.

Droits de reproduction — Lorsqu'un article contient de la documentation (tableaux, figures, schémas, etc.) déjà publiée, il incombe à l'auteur d'obtenir **une permission écrite du titulaire de ces droits d'auteur** pour permettre la reproduction de l'information **en format imprimé et électronique**. La lettre d'autorisation doit accompagner le manuscrit soumis, sans quoi le

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processus de publication pourra être retardé. Cette lettre sera exigée avec toute mention du type « Tirée de... ». Si une illustration est modifiée, de sorte qu'une telle autorisation n'est pas requise, la formulation doit être explicite : « Modifiée d'après... ». Si l'illustration est reconstituée à partir d'informations tirées d'autres auteurs la mention doit être du même type que pour une référence.

Soumission de la version approuvée — Les auteurs sont priés de soumettre **une copie imprimée ainsi qu'une copie sur disquette de la version approuvée de l'article seulement**. Les fichiers de texte et les fichiers d'illustrations devront être soumis sur des disquettes distinctes. Le nom des auteurs doit être indiqué clairement sur chaque disquette soumise. Le **texte** (y compris les tableaux) devrait être soumis en format de traitement de texte (WordPerfect, Microsoft Word ou TeX est préférable, compatible à IBM ou Macintosh). Les macros en TeX et la documentation pour la préparation des soumissions sont maintenant disponibles à ftp://ftp.tex.ac.uk/tex-archive/macros/latex/contrib/supported/nrc/, ftp://ftp.dante.de/tex-archive/macros/latex/supported/nrc/ et ftp://ctan.tug.org/tex-archive/macros/latex/contrib/supported/nrc/. Il importe d'indiquer le logiciel de traitement de texte utilisé, la version, de même que le type d'ordinateur (IBM ou Macintosh). En ce qui a trait aux **illustrations**, il convient de se reporter à la section « Préparation des fichiers électroniques des illustrations ». Tout article devra être accompagné d'une lettre faisant foi du fait que la version du texte sur disquette reflète exactement la version imprimée soumise.

Épreuves en placard — Une épreuve en placard, des épreuves des illustrations, une copie de l'article corrigé et un bon de commande de tirés à part sont envoyés à l'auteur correspondant. **Les épreuves en placard doivent être relues attentivement car elles ne sont pas corrigées par les Presses scientifiques du CNRC.** Elles doivent en outre être retournées dans les 48 h suivant leur réception. Au stade des épreuves, il n'est plus temps d'apporter des modifications importantes ni de faire des ajouts ou des suppressions. Les frais occasionnés par des modifications excessives devront être assumés par les auteurs.

Tirés à part — Pour obtenir des tirés à part, il est nécessaire de remplir le bon de commande à cet effet et de le retourner avec le paiement (chèque, numéro de carte de crédit, numéro du bon d'achat ou pièce de journal interne) en même temps que les épreuves et l'article corrigés. Le tarif des tirés à part commandés après la parution du numéro du Journal est fortement majoré. **Le Journal n'offre pas de tirés à part gratuits; ceux-ci ne sont postés qu'après réception d'un numéro du bon d'achat ou du paiement.**

Transfert des droits d'auteur — Tous les auteurs doivent compléter un formulaire de transfert des droits d'auteur au CNRC. On obtiendra ces formulaires auprès de la directrice scientifique principale, dans le premier numéro de chaque volume ou sur le site Web des Presses scientifiques du CNRC.

Toute **permission de republication** partielle ou intégrale d'un article doit être obtenue auprès des Presses scientifiques du CNRC.

Préparation des manuscrits

Directives générales

Le processus de publication sera grandement facilité si les articles sont préparés conformément au style du Journal.

Dactylographiez le manuscrit sur papier blanc (21,6 sur 27,9 cm (8,5 sur 11 po)) sur un côté de la page. Laissez toujours une marge d'au moins 2,5 cm (1 po). Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs et les renvois qui s'y rapportent. Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations. Tout le manuscrit, y compris tableaux, légendes des tableaux et des figures, renvois et liste de références, doit être dactylographié à **double interligne**. N'utiliser l'italique que pour les passages qui doivent paraître en italique dans le document final. En aucun endroit du manuscrit n'écrivez entièrement en majuscules. Pour les références citées dans le texte, utilisez le système nom et année.

Dispositions générales

L'orthographe doit suivre *Le Grand Robert*. Les accents doivent être insérés sur les majuscules. Les auteurs sont responsables de l'uniformité de l'orthographe.

Le *CBE Manual for Authors, Editors, and Publishers : Scientific Style and Format* (6e éd., 1994, Council of Biology Editors, Inc., Chicago, IL 60603, É.-U.) sert de guide quant à la forme de la présentation. Les titres de périodiques sont abrégés suivant *BIOSIS® Serial Sources* (BIOSIS, 2100 rue Arch, Philadelphia, PA 19103-1399, É.-U.). C'est la responsabilité des auteurs de s'assurer que leurs références sont complètes et exactes. Pour les noms de poissons et leur orthographe, le Journal suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (5e éd., 1991, Spec. Publ. No. 20, American Fisheries Society). Pour la nomenclature génétique pour les locus de codage des protéines, le Journal suit les recommandations contenues dans Shaklee et al. (1990, Trans. Am. Fish. Soc. **119** : 2–15). Il est recommandé de se servir du **Système international d'unités** ou, tout au moins, de fournir les équivalences en unités SI. Ce système est décrit dans le *Guide de familiarisation au système métrique*, publié en 1989 par l'Association canadienne de normalisation (178, boulevard Rexdale, Etobicoke, ON M6N 3T3, Canada). Pour des raisons pratiques, on permet certaines exceptions à l'utilisation du Système international d'unités (comme dans un éditorial du Journal, vol. 40, n° 12).

Liste de contrôle pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs :

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes aux buts de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou à l'intérieur du texte? Est-ce que certaines données devraient être présentées séparément dans un rapport manuscrit ou dans un dépôt de données?

Si une analyse statistique est effectuée, la statistique cède-t-elle le pas à la recherche? Dans des énoncés de probabilité, les tableaux statistiques inutiles sont-ils exclus et seulement les tests statistiques cités?

Le texte gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le **titre** est-il représentatif du contenu du rapport? Le **Résumé** donne-t-il l'essentiel des connaissances nouvelles? L'**Introduction** se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème? La section **Matériel et méthodes** contient-elle le minimum de détails qui permettront aux lecteurs de saisir les grandes lignes de l'étude et de juger de la valeur des données? Les généralisations sur les **Résultats** sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions? La **Discussion** est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Sont énumérés, ci-dessous, des façons d'éviter les problèmes techniques les plus communs dans la soumission des manuscrits. En accordant une attention particulière à ces points lors de la préparation de leurs manuscrits, les auteurs peuvent accélérer le traitement des articles.

(1) Limiter le résumé à un paragraphe d'environ 175 mots.
(2) Dactylographier à double interligne tous les éléments du manuscrit, y compris la bibliographie et les légendes des tableaux et des figures.
(3) Éviter partout l'emploi exclusif de majuscules, y compris dans les en-têtes et les légendes des tableaux et des figures.
(4) Ne composer en italique que les noms latins d'organismes

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et certaines notations statistiques et mathématiques qui devront être imprimés en italique.

(5) Dans les figures, les tableaux et le texte, exprimer les unités de mesure par leurs symboles SI propres. Pour les nombres inférieurs à l'unité, placer un zéro avant la virgule décimale.

(6) Éviter les formes ambiguës, telles que g C/m^2/jour; utiliser plutôt g C·m^{-2}·jour^{-1}.

(7) Identifier le test qui a servi à évaluer la signification statistique, donnant également la valeur de probabilité. S'il s'agit de tests communs, il n'est pas nécessaire d'en donner la référence.

(8) Dans le texte, généraliser à partir des tableaux et des figures; éviter une répétition de tous les détails. S'assurer que tous les tableaux et figures sont indépendants et mentionnés dans le texte dans l'ordre numérique. Les légendes doivent indiquer le but du tableau ou de la figure.

(9) Préparer la section des remerciements au stade du manuscrit et non à celui des épreuves.

(10) En référant à des communications personnelles, donner les initiales et l'adresse postale de la personne en cause.

(11) Éliminer toutes références qui ne s'appliquent pas directement au problème.

(12) Vérifier soigneusement la correspondance des références en regard des citations dans le texte et vice versa. Dans le cas de matériel difficilement accessible, indiquer l'endroit où le trouver (p. ex. disponible auprès du Département de biologie, Université Laval, Sainte-Foy, QC G1K 7P4, Canada).

(13) Éliminer les virgules entre le nom et la date dans les citations telles que (Smith 1990) et ne pas souligner ni mettre en italique « et al. ».

(14) Aux fins de la révision, les photocopies des figures, sauf pour les demi-teintes, sont appropriées. Sur demande, lorsqu'il s'agira de publier l'article, envoyer des photographies, des imprimés laser ou les dessins originaux/fichiers électroniques des figures (voir « Illustrations » et « Préparation des fichiers électroniques des illustrations »). Utiliser autant que possible un lettrage uniforme.

Parties du manuscrit

Organisation

Organiser le manuscrit par rapport au but ou à la portée de l'étude, tels qu'énoncés dans l'introduction. Il est particulièrement important que le titre et les sous-titres soient en harmonie avec les objectifs.

Avant de commencer la rédaction du manuscrit, dresser une liste provisoire des sous-titres ou en-têtes, avec le moins de divisions possible. Retoucher les jusqu'à ce qu'ils semblent assurer, pour le lecteur, une marche logique; ordinairement, l'ordre chronologique ne sera pas satisfaisant. Il sera plus facile d'évaluer les résultats si méthodes, résultats et discussion sont décrits dans des sections séparées.

Organiser les tableaux et les figures de façon à faciliter les comparaisons, groupant les données apparentées en aussi peu de tableaux et de figures que possible. S'assurer que ces derniers sont aussi clairs que possible sans référence au texte.

Commencer les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés particuliers. Si la conclusion est donnée d'abord puis appuyée ensuite, non seulement le travail sera plus facile à lire, mais aussi les autres scientifiques pourront plus aisément en évaluer les résultats. Dans la rédaction des manuscrits, le défaut le plus commun est d'omettre de donner, au début, les généralités les plus dignes de mention.

Voir à ce que le matériel de chaque section soit pertinent à l'en-tête et que le matériel de chaque paragraphe se rapporte à la première phrase introduisant le sujet.

Avant de rédiger les paragraphes, composer la phrase thème de chaque paragraphe et disposer ces phrases dans l'ordre approprié.

Titre

Limiter le titre à ce que l'étude veut démontrer. C'est la clé de l'article et il devrait refléter clairement et brièvement le contenu de l'étude. Le titre a deux fonctions : (1) il permet au lecteur de juger si, oui ou non, l'article peut avoir un intérêt et (2) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance potentielle de l'article. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, au besoin, la méthode d'approche technique (p. ex., rayons X, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que « Sur » ou « Vers », ou des expressions telles que « Contribution à… » ou « Recherche sur… ». De bons titres facilitent le classement des publications et leur utilisation par les scientifiques et les bibliothécaires. On évitera les titres en séries.

Résumé

Un résumé doit accompagner chaque texte et exposer brièvement, en 175 mots ou moins, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé. Les auteurs qui peuvent soumettre des résumés dans les deux langues officielles du Canada, c'est-à-dire en français et en anglais courants, sont encouragés à le faire.

Comme le titre, le résumé permet aux lecteurs de prendre connaissance du contenu de l'article et de décider si, oui ou non, il leur faut lire ce dernier en entier. Indiquer, au début du résumé, la principale conclusion de l'étude et l'appuyer par des découvertes pertinentes. Ne donner que les détails des méthodes nécessaires à la compréhension de ce qui a été fait et les insérer dans l'énoncé des découvertes. Éviter l'emploi de phrases telles que « … on y analyse » ou « … a été trouvé » ; être plus spécifique. Comme le résumé est souvent séparé du corps principal de l'article par les services d'analyse et de classement, c'est la seule partie d'un travail que certains lecteurs auront l'occasion de voir; il importe donc qu'il reflète précisément le contenu du travail et qu'il soit complet en lui-même (c.-à-d., les références absolument *essentielles* sont indiquées, sous forme retraçable, p. ex., R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. **37** : 268–282).

Introduction

Limiter l'introduction à la portée, au but et à la raison de l'étude. Ne mentionner que les travaux publiés et autres informations nécessaires à la définition du problème et à la perspective du travail. Commencer avec le but ou la portée du travail, définir ensuite le problème et ajouter ici et là des jalons qui aideront à orienter le lecteur. En général, une introduction n'a pas besoin de dépasser 375–500 mots.

Matériel et méthodes

Cette section renferme ce dont on a besoin pour trouver réponse aux questions soulevées dans les objectifs du travail.

Limiter les renseignements à ce qui est nécessaire pour juger de la validité des découvertes. Cette évaluation sera facilitée si toute l'information est présentée, autant que possible, dans une section. S'il s'agit d'outillage ou de techniques déjà publiés, référer aux publications et ne décrire en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phrase qui en indique le but, comme : « Afin de déterminer… nous… ». Si la section est longue, utiliser des sous-titres correspondant à ceux de la section des résultats.

Résultats

Limiter les résultats aux réponses apportées aux questions en rapport avec le but de l'étude; que ces réponses soient aussi complètes que possible, tout en étant concises. Exprimer, autant

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que possible, les découvertes dans les mêmes termes que les observations ou les mesures, évitant ainsi de confondre faits et spéculations. Dégager les généralités des tableaux et des figures et y référer en évitant de répéter dans le texte ce que les légendes devraient exprimer clairement. Le matériel complémentaire au texte peut être classé dans les séries de rapports ou dans un dépôt de données reconnu; et on y référera dans le texte.

Discussion

Limiter la discussion à l'énoncé de la principale contribution de l'étude et à l'interprétation de découvertes particulières, les comparant avec celles d'autres auteurs. On continuera à mettre l'accent sur la synthèse et l'interprétation, ainsi que sur l'exposition de généralisations et de principes largement applicables. S'il s'agit d'exceptions ou de points douteux, les noter et faire ressortir la manière dont les résultats corroborent ou contredisent les travaux déjà publiés. Limiter la spéculation à ce qui peut être appuyé sur des preuves raisonnables. Terminer cette section par un court résumé de l'importance du travail et des conclusions auxquelles il a conduit. Si la discussion est brève et précise, elle peut être combinée avec les résultats en une seule et même section.

Remerciements

Nous recommandons fortement aux auteurs de limiter les remerciements aux personnes qui ont contribué d'une manière substantielle aux aspects scientifiques et techniques de l'article, fourni une aide financière ou amélioré la qualité de la présentation. Éviter de mentionner les personnes qui n'ont fourni qu'un travail de soutien.

Bibliographie

On choisira les références avec soin, les limitant aux publications importantes. On ne peut citer dans cette section les références à des données inédites, manuscrits en préparation ou soumis à d'autres périodiques, états des travaux et communications inédites présentées à des réunions annuelles. On peut toutefois les mentionner dans le texte à titre de données inédites ou de communications personnelles (incluant les adresses). Si l'on doit citer des rapports d'experts-conseils ou d'autres documents dont la distribution est limitée, on devra préciser l'endroit où l'on peut se les procurer. **On doit s'assurer que les références mentionnées dans le texte correspondent à celles qui sont contenues dans la bibliographie et vice versa.** Presque tous les manuscrits soumis au Journal contiennent des erreurs dans cette section.

Notes infrapaginales

Les notes infrapaginales ne devraient figurer dans le texte que lorsqu'elles sont inévitables, mais leur utilisation dans les tableaux est encouragée. Lorsque les notes infrapaginales figurent dans le texte, leurs appels devraient être désignés par des chiffres arabes en exposant (sauf dans le cas des tableaux, voir ci-dessous) et numérotés consécutivement à partir de la première note infrapaginale, y compris toute note apparaissant en page titre. Chaque note doit figurer au bas de la page où elle est signalée, **pas dans la bibliographie**.

Équations

Les équations doivent être dactylographiées clairement, à triple interligne si elles incluent des exposants ou des indices. Les exposants et les indices doivent être lisibles et correctement placés. Il convient de faire une distinction entre la lettre *l* et le chiffre *un*, et entre la lettre majuscule *O* et le chiffre *zéro*. Une lettre ou un symbole ne devrait représenter qu'une seule entité et devrait être utilisé de façon uniforme dans l'article. Chaque variable doit être définie dans le texte ou dans une **liste des symboles** devant apparaître après la bibliographie. Les variables représentant des vecteurs, des matrices, des matrices vectorielles et des tenseurs doivent être clairement définies. Les numéros d'équation doivent être identifiés par des chiffres arabes placés entre parenthèses et alignés avec la **marge de gauche**. Aucune distinction n'est faite entre la numérotation des formules mathématiques et celle des formules chimiques.

Tableaux

Les tableaux sont utilisés pour présenter des données qui se répètent et devraient occuper le moins d'espace possible. Agencez les tableaux de façon qu'ils s'adaptent soit à une ou deux colonnes du Journal. Dactylographiez chaque tableau sur une page séparée et numérotez-les en chiffres arabes. Tracez des lignes horizontales de part et d'autre des en-têtes et au-dessous des colonnes, mais rarement ailleurs. N'utilisez jamais de lignes verticales. Laissez plutôt des espaces supplémentaires. Chaque tableau doit avoir une légende instructive, complète et indépendante. Les renvois des tableaux doivent être indiqués par des minuscules suscrites dactylographiées au bas du tableau. Placez les tableaux après la bibliographie. Notez que les *tableaux dans le texte* ne sont pas numérotés et sont dactylographiés dans le corps du texte. Ils ont rarement besoin de lignes horizontales.

Appendices

Les appendices doivent être indiqués de façon séquentielle (p. ex., A, B, C, etc.). Les illustrations et les tableaux en appendice doivent être numérotés différemment des illustrations et des tableaux du corps de l'article (p. ex., figure A1, tableau A1, etc.).

Documentation complémentaire

Le Conseil national de recherches du Canada administre un Dépôt des données non publiées dans lequel la documentation complémentaire peut être versée, à la demande des auteurs ou la directrice scientifique principale. De plus, il est maintenant possible d'accéder à cette documentation dans le format de son fichier d'origine à partir du site Web du Journal. L'accès se fera par le biais d'un hyperlien apparaissant dans la page Web de l'article pertinent. La documentation complémentaire peut comprendre de grands tableaux, des calculs complexes et des cartes détaillées qui ne sont pas essentiels à la compréhension ou à l'évaluation du document. Les auteurs qui désirent utiliser ce service doivent clairement indiquer les parties dont ils demandent le dépôt dès la soumission de leur article. Les tableaux et les figures doivent être numérotés de façon consécutive, distinctement de ceux destinés à la publication (p. ex., figure D1, tableau D1). Toute donnée déposée doit faire l'objet d'une note infrapaginale à la section appropriée du document. Des copies des données déposées peuvent être obtenues contre paiement auprès du Dépôt des données non publiées, ICIST, Conseil national de recherches du Canada, Ottawa, ON K1A 0S2, Canada.

Illustrations

Fournir des photographies, des imprimés laser (les imprimés par imprimante par points sont inacceptables) ou les dessins originaux (pourvu qu'ils ne dépassent pas 27,9 sur 43,2 cm (11 sur 17 po)) de chaque illustration. Transmettre trois copies des illustrations qui serviront au moment de la révision.

Chaque figure ou groupe de figures doit être préparé de manière à occuper, après une réduction appropriée, l'espace d'une ou deux colonnes du texte. Les dimensions finies maximales d'une illustration sur une colonne sont de 8,8 sur 23,9 cm (3,5 sur 9,4 po) et celles d'une illustration sur deux colonnes est de 18,2 sur 23,9 cm (7,2 sur 9,4 po). Les figures (y compris les similigravures) sont numérotées en chiffres arabes selon leur ordre séquentiel et doivent être annoncées dans le texte bien que tous leurs éléments doivent être intelligibles en eux-mêmes. Tous les termes, les abréviations et les symboles qui se trouvent dans les figures doivent être les mêmes que ceux apparaissant dans le texte. Seuls les détails essentiels devraient être identifiés; l'information plus détaillée devrait paraître dans la légende. Chaque illustration doit être identifiée, de préférence au bas, à gauche, par le numéro de la figure et les noms des auteurs, suffisamment éloignés de l'espace réservé à l'illustration.

Les **dessins au trait** originaux doivent être en encre noire ou produits par ordinateur en encre noire sur du papier blanc de

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première qualité ou un matériau comparable. Quant aux graphiques produits par ordinateur, il faut fournir un imprimé au laser de la meilleure résolution disponible. **Les photocopies ne sont pas acceptables.**

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Les **cartes** doivent avoir des motifs clairs et gras, et comporter les longitudes et latitudes (ou les coordonnées de Mercator transverses universelles) de même qu'une échelle graphique. Sur **les cartes du Québec**, les noms officiels des municipalités doivent être utilisés (p. ex., Québec, Montréal et Clarke City) et les entités géographiques doivent être présentées en français (p. ex., Lac Bienville), à l'exception de celles qui sont d'intérêt pancanadien — ces dernières, qui ont un nom officiel dans les deux langues (p. ex., Atlantic Ocean et océan Atlantique), se doivent de respecter la langue de l'article. Pour obtenir une liste complète des noms des régions d'intérêt pancanadien, consultez Le guide du rédacteur (p. 236–237, 2e éd., 1996), publié par les Travaux publics et Services gouvernementaux Canada, Ottawa, ON K1A 0S5, Canada.

Les **photographies** doivent être en *demi-teintes* sur papier glacé. Les épreuves doivent être de première qualité, sur papier glacé, avec contrastes bien marqués. Les copies destinées à la reprographie doivent être rognées de façon à ne laisser paraître que les éléments essentiels et être montées sur carton bristol blanc **léger** et flexible. Aucun espace ne doit paraître entre les photographies constituant une même planche. Une photographie ou un groupe de photographies doit être préparé de manière à occuper, **sans réduction supplémentaire**, une ou deux colonnes du texte. Les micrographies électroniques et les photomicrographies doivent comporter une échelle graphique à même l'illustration. On évitera les pertes de détails et de contraste inhérentes au procédé d'imprimerie en agençant le contraste et la densité de toutes les photographies montées sur une même planche.

Les **illustration en couleurs** sont aux frais de l'auteur. On peut obtenir de plus amples renseignements sur les prix auprès de Cecily Pearson, rédactrice administrative du Journal (613-993-9099; télécopieur : 613-952-7656; courriel : cecily.pearson@nrc-cnrc.gc.ca).

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Préparation des fichiers électroniques des illustrations

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Le logiciel graphique préféré par les Presses scientifiques du CNRC est CorelDraw! Pour les autres applications possibles, reportez-vous à la « Liste des programmes graphiques électroniques » à http://pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_prog_f?cjfas_graphics_f.html.

Toutes les illustrations doivent être soumises dans leur dimension de tirage final. Quant aux figures comportant plusieurs parties (p. ex., *a*, *b*, *c*, *d*, etc.) crées sur le même logiciel, elles doivent être assemblées dans un seul fichier plutôt que de transmettre plusieurs fichiers.

Il faut **garder** les illustrations le plus simple possible afin d'éviter les embûches. Éviter les textures et les fonds grisés compliqués, particulièrement dans les programmes d'illustration vectorielle.

Fichier en mode point — Les fichiers d'images en mode point sont produits sur une grille dans laquelle chaque carré (ou pixel) correspond à une nuance de noir, de couleur ou de gris. Un fichier en mode point est défini par le nombre de pixels ou d'éléments par pouce. Comme le pixel est défini comme un point, on parle aussi de « points par pouce » ou « ppp ». Plus la résolution de l'image est grande, plus le nombre de points sur une surface donnée est élevé.

Les illustrations soumises en mode point doivent être de définition adéquate. Les exigences minimales de définition sont les suivantes : 600 ppp pour les dessins au trait et les lignes fines (les dessins au trait comportant des lignes fines ou un fond grisé), 300 ppp pour les demi-teintes et les couleurs et 600 ppp pour les combinaisons (demi-teintes avec lettrage à l'extérieur de l'espace réservé à la photo).

Tous les fichiers en *couleurs* soumis doivent suivre la base CMJK (cyan, magenta, jaune et noir). Ces couleurs sont utilisées dans l'impression commerciale tout en couleur. Les graphiques RVB (le rouge, le vert et le bleu sont les couleurs utilisées particulièrement pour produire les images sur un écran) ne s'impriment pas correctement.

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Conventions

Abréviations

N'abréger les termes désignant les unités de poids et mesures dans le texte que lorsqu'ils sont précédés d'un nombre.

becquerel (Bq)
calorie (cal)
centimètre (cm)
centimètre carré (cm^2)
centimètre cube (cm^3)
centimètres par gramme par seconde ($cm \cdot g^{-1} \cdot s^{-1}$)
coulomb (C)
décimètre (dm)
degré Celsius (°C)
degrés de liberté (dl)
écart type (ET)
électronvolt (eV)
erreur type (ErT)
farad (F)
gramme (g)
hectare (ha)
hertz (Hz)
heure (h)
joule (J)
kilomètre (km)
litre (L)
lumen (lm)
lux (lx)
mètre (m)
mètre carré (m^2)
mètre cube (m^3)
micromètre (µm)
milligramme (mg)

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millilitre (mL)
millimètre (mm)
millimètre carré (mm^2)
minute (min)
masse molaire (M)
mole (mol)
moles par litre (mol/L, M)
pascal (Pa)
seconde (s)
tonne (métrique) (t)
volt (V)
volume (vol)
watt (W)

Dates

On écrira les dates dans l'ordre jour–mois–année, p. ex. 9 octobre 1983, sans virgule entre le mois et l'année.

Citations de références dans le texte

Système de nom et année

Le Journal utilise le système de nom et année, c.-à-d. que le nom de l'auteur ou des auteurs et l'année de publication sont insérés dans le texte à un endroit approprié : « Brown (1983) compare… » ou « …on a comparé (Brown 1983) ». Si la référence comporte plus de deux auteurs, inscrivez le nom du premier auteur seulement, suivi de « et al. » : « Brown et al. (1983) comparent… » ou « …on a comparé (Brown et al. 1983) ».

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Données inédites

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Bibliographie

Les références doivent être classées par ordre alphabétique des noms des premiers auteurs. Si la liste comprend plusieurs publications d'un même premier auteur, les règles suivantes seront appliquées. (1) S'il n'y a qu'**un auteur**, les ouvrages se succèdent par ordre chronologique de partition en commençant par le plus ancient. Si l'auteur a publié, au cours d'une année, plusieurs livres ou articles, on distinguera les références les unes des autres en faisant suivre l'année de publication d'une lettre (*a*, *b*, *c*, etc.). (2) S'il y a **deux auteurs**, les ouvrages sont placés à la suite de ceux n'ayant qu'un auteur, et sont alors classés par ordre alphabétique du nom du deuxième auteur. (3) S'il y a **trois auteurs ou plus**, les ouvrages sont placés à la suite de ceux ayant deux auteurs et sont classés par ordre chronologique.

La liste qui suit donne des exemples de ponctuation, de style et d'abréviations utilisés dans les références bibliographiques (d'après *CASSI* ou *BIOSIS® Serial Sources*).

Article d'une revue

Archambault, D., et Bourget, E. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieux subarctiques. Can. J. Fish. Aquat. Sci. **40** : 1278–1292.

Numéro complet d'une revue

Gordon, D.C., Jr., et Hourston, A.S. (*Directeurs de la rédaction*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40**(suppl. 1).

Livre dans une série

Scott, W.B., et Crossman, E.J. 1974. Poisons d'eau douce du Canada. Bull. can. sci. halieut. aquat. n° 184.

Livre ne faisant pas partie d'une série

Forrester, W.D. 1983. Manuel canadien des marées. Service hydrographique du Canada, ministère des Pêches et des Océans, Ottawa.

Partie d'un livre

Aubert, M., Aubert, J., Daniel, S., et Desirotte, N. 1982. État actuel de la pollution bactérienne au large des côtes françaises. *Dans* La pollution des mers et les ressources biologiques. *Sous la direction de* M. Ruivo. Fishing News (Books) Ltd., Londres. p. 36–40.

Corporation auteur

American Public Health Association, American Water Works Association et Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14e éd. Washington.

Thèse

Delisle, C. 1969. Écologie, croissance et comportement de l'éperlan du Lac Heney, Comté de Gatineau ainsi que la répartition en eau douce du Québec. Thèse de doctorat, Université d'Ottawa, Ottawa.

Rapport

Dutil, D.J., Fortin, M., et Vigneault, Y. 1982. L'importance des zones littorales pour les ressources halieutiques. Mémoire remis au Conseil consultatif de l'environnement du Québec. Rapp. manuscrit can. sci. halieut. aquat. n° 1653.

Traduction

Koike, A., et Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64** : 1–11. [Traduit du japonais par Can. Transl. Fish. Aquat. Sci. n° 4950, 1983.]

Liste de mots

Cette section, dans la version anglaise du Guide, contient une série de mots dont l'orthographe pose certains problèmes d'uniformité, comme, p. ex., « cold water » (nom) « cold-water » (adjectif); « hard water » (nom) « hardwater » (adjectif), etc. L'auteur préparant un texte en anglais est prié de consulter la version anglaise du Guide.

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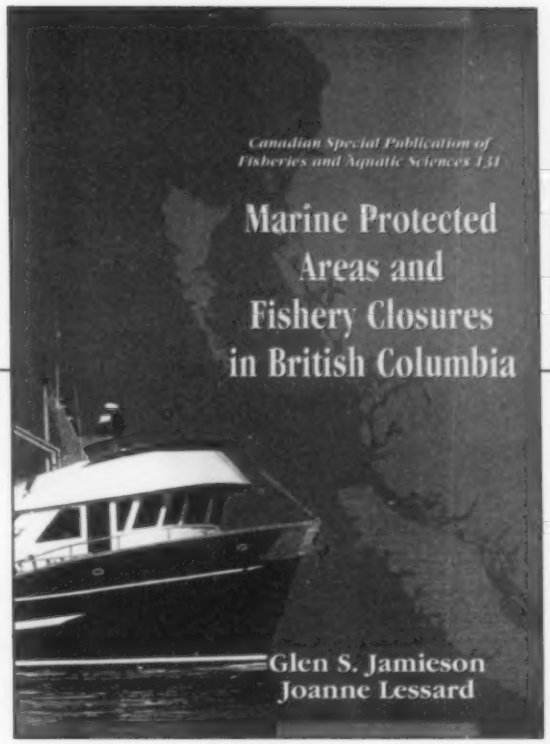
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R.J. Beamish, D.J. Noakes, D.L.G. Noakes, and F.W.H. Beamish — **iii–v** — William Edwin Ricker, OC, FRSC, LLD, DSc

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